The Journal of ARACHNOLOGY

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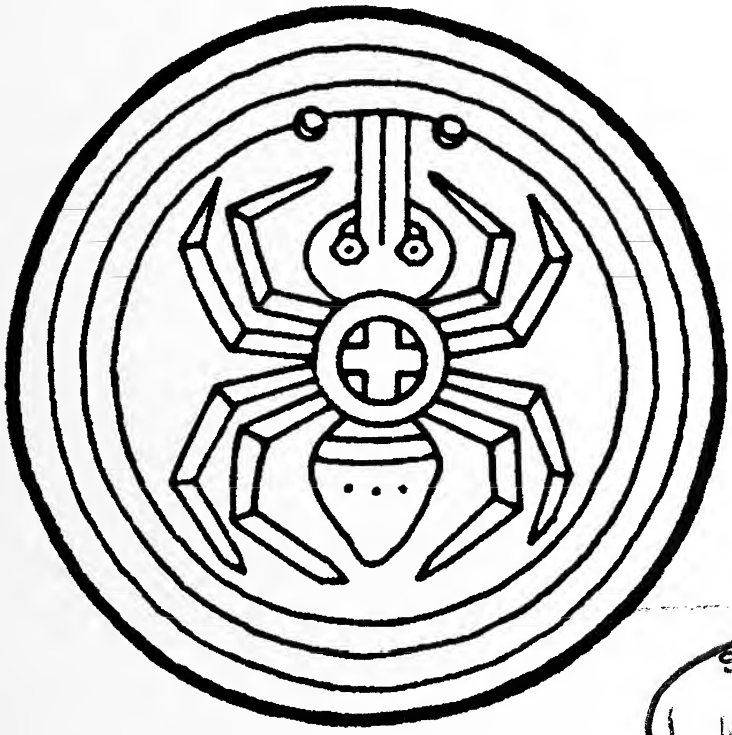

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Cover photo: Shell gorget of spider on web from an archeological site in Fulton County, Illinois. Used with permission.

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SUB-FOSSIL SPIDERS FROM HOLOCENE PEAT CORES

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ABSTRACT. An attempt was made to recover identifiable spider sub-fossils from peat cores taken from a post-glacial basin mire in Cheshire, north-west England. Although the features normally required to identify specimens to species level in taxonomic keys were rarely preserved, carapace morphology and cheliceral dentition allowed unequivocal identification to species level in many cases. Current lack of knowledge of the autecology of wetland spiders prevents any conclusion regarding the paleoecological conditions, but the technique could reveal insights into the post-glacial development of the spider faunal assemblage of mires.

Keywords: Spiders, sub-fossils, peat, chelicerae

The value of undisturbed peat deposits as datable sediment is well recognized and the pollen record has been widely used to study the post-glacial vegetational succession, climatic change and the development of agricultural activity during the last 10,000 years (the Holocene epoch). This technique depends on the remarkable resistance of the exine of pollen grains to natural decay and the chemical digestions used in their recovery, together with the taxonomic value of their morphology.

It is also recognized that identifiable (although disarticulated) invertebrate remains can be recovered from peat and other unconsolidated sediments to give useful palaeoecological information. This has been particularly successful in the case of beetles which have a heavily sclerotized exoskeleton that is resistant to decay and bears surface details which enable identification to species level (Coope 1965). Also many beetle species can be linked closely to habitats.

Hofmann (1986) was able to retrieve the head capsules of *Chironomus* larvae by essentially the same method used for pollen analysis. Chironomid larvae and their exuviae would have been particularly numerous in peat and the head capsules are well sclerotized, but as I had observed the rapid disarticulation and decomposition of spiders in pitfall traps when flooding had diluted the preservative, it seemed unlikely that identifiable spider remains would be preserved.

Keys for the identification of spider species have required, among other things, microscopy of the mature female epigyna and male palps. These are not always well sclerotized and would, in any case, require some expertise to recognize if distorted and out of context. However, Coope (1965, 1986) suggested that (in the case of beetles) fragments of cuticle may be identifiable if a well determined reference collection is available. The taxonomic usefulness (at the supra-specific level) of other morphological characters of spiders, has been reviewed by Lehtinen (1978), and these include eye patterns, cheliceral armature and leg structure.

As a reference collection of peatland spiders, appropriate to the study area, was available to the author, he decided to attempt the retrieval of identifiable spider sub-fossils from a species-rich basin mire in Cheshire, England.

METHODS

Site description.—Several samples were taken from the basin mire at Wybunbury Moss National Nature Reserve, Cheshire, England (National Grid Reference: SJ697503), on a transect described by Green & Pearson (1977) and for which a stratigraphy was available. This site is in an area of northwest England which has an oceanic climate and glacial drift geology which have favored the development of numerous basin and raised mires.

Core sampling.—The total depth of peat at the study site is about 5 m, representing accumulation over 5000 years. Sampling depths were 650–750 mm (ca. 500 yr BP), 1150–1250 mm (ca. 1000 yr BP) and 1650–1750

mm (ca. 1400 yr BP), these being the bottom 100 mm of each sequential core. This chronology is derived from the peat accumulation rate suggested for this site by Green & Pearson (1977). The samples were obtained by using a 'Russian pattern' peat sampler (Jowsey 1966; Aaby & Digerfeldt 1986), which produces half-cylinders of peat with a diameter of about 2.5 cm and length of 50 cm (Fig. 1).

Extension rods can allow sampling to more than 5 m if sufficient manpower is available to insert and withdraw the sampler at this depth but, for this single-handed investigation, the maximum depth used was 1.75 m. The surface vegetation was cut away before coring, to minimize the possibility of contamination with recent material.

Aaby & Digerfeldt (1986) described the procedure as shown in the inset cross-sections of Fig. 1: inserting the tool with the cutting shell over the rib and then an anti-clockwise rotation to cut a half-cylinder of peat. Jowsey (1966), on the other hand, performed the reverse action, a clockwise rotation of the cutting shell producing quarter-cylinders of peat on either side of the rib. The method of Aaby & Digerfeldt was used, because insertion with the rib exposed increased the difficulty of penetrating the upper layer which contains tough roots of *Eriophorum* and *Erica*. Samples were returned to the laboratory in 'zip-seal' plastic bags. Should finer stratigraphic resolution be required, then the intact cores can be laid in split plastic pipes and wrapped in cling-film.

Extraction of arthropod remains followed a modified scheme of Coope (1986). Half kilogram aliquots of the peat (larger amounts clogged the sieves) were dispersed in warm water and the coarser material removed by washing through a 2 mm mesh sieve, the material passing through being collected on a 250 μm mesh sieve of 20 cm diameter. The drained, but still damp, product was transferred to a large bowl and mixed thoroughly for several minutes with its own volume of paraffin (kerosene). This can be done by rubber-gloved hand or with a table fork or similar implement.

After decanting as much surplus paraffin as possible (which can be reused), water is added to the mixture, with stirring, to resuspend the sample and fill the container. After ca. 1 hour the sample will have divided into sedimented and floating fractions. The floating fraction is transferred, either by decanting or spooning off, to another sieve of smaller mesh (I used 53 μm) and most of the residual paraffin can be removed by rinsing with warm water containing detergent.

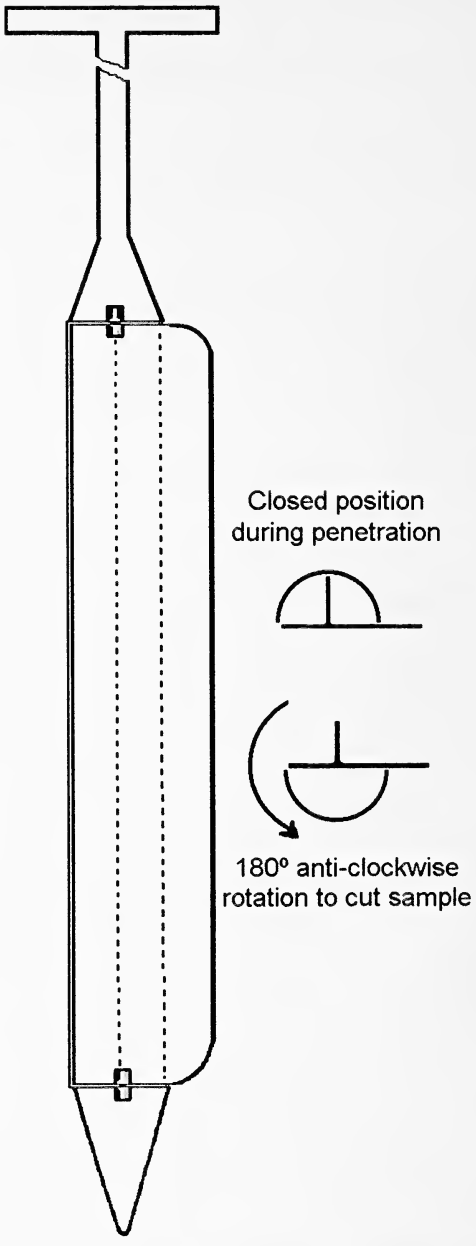


Figure 1.—The 'Russian pattern' peat corer (after Aaby & Digerfeldt 1986).

Coope (1986) then suggested a final rinse in alcohol, followed by microscopy of the extracted material in alcohol. While this may have worked well with the organic silts that

Table 1.—Summary of sub-fossil retrieval. Level 1 samples are from 650–750 mm depth (ca. 500 yr BP); Level 2 samples are from 1150–1250 mm depth (ca. 1000 yr BP) and Level 3 samples are from 1650–1750 mm depth (ca. 1400 yr BP).

	Level		
	1	2	3
Amount of peat processed	5 kg	0.5 kg	0.5 kg
Carapaces	59	5	
Sternums	22	1	1
Chelicerae	130	2	3
Male palps	4	1	
Palpal tibiae			1
Epigyna	1		

he was studying, the floating fraction from partially humified peat samples was often bulky and contained much vegetable material. It was found that resuspending the floating fraction in clean water, after the detergent rinse, caused most of the vegetable matter (sphagnum leaves) to sink.

The new floating fraction was transferred to a petri dish without alcohol treatment for microscopy. Items of interest could be picked from the surface of the water with fine forceps and transferred to alcohol. Best visibility of the sub-fossils (many of which are transparent and pale in color) was obtained by using a mixture of transmitted and incident illumination. A mechanical stage with X and Y axis controls is useful for scanning the surface of the water in a systematic manner.

RESULTS

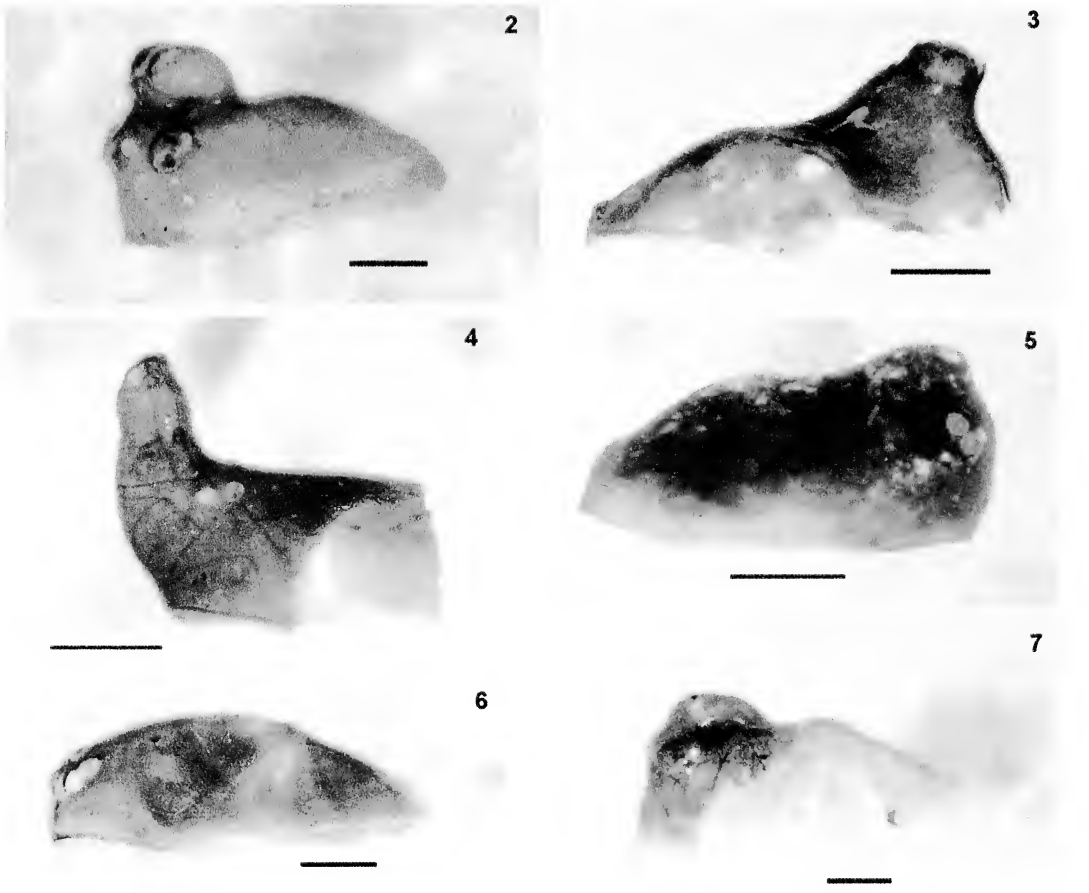
The bulk of the recognizable invertebrate remains consisted of large numbers of oribatid mites, larval head capsules from several insect orders including Odonata and Diptera, beetle elytra and ant mandibles. Spider remains included fragments of carapace, sternum and leg segments, but rather more numerous, and of potential taxonomic use, were individual chelicerae, some complete with articulated fang. The final yield of spider material is shown in Table 1. The data shown in the table might suggest that the occurrence of sub-fossils, especially chelicerae, declined as depth increased. This is probably an artifact, because the sub-samples from the two lower levels were obtained on the first site visit and were the first to be processed. There is a strong subjective impression that the yield improved with experience of the technique, especially at the microscopy stage. Chelicerae, at low magnification, could have been confused with small leg segments, such as trochanters from other arthropod taxa, and ignored. There seems no reason to doubt that similar yields of spider sub-fossils would be available throughout the peat column.

Identification of sub-fossils.—Spider species that were identifiable from sub-fossils came from the following categories: linyphiid males that had distinctive head modifications; larger species from which male palps or female epigynes survived; larger species with distinctive cheliceral dentition; larger species with distinctive carapace features such as eye pattern, hair and bristle distribution, overall size and shape or some combination of these.

Some of the more interesting sub-fossils obtained from the material collected at Wybunbury Moss are shown in Figs. 2–19. It is notable that three small linyphiid species were identified (Figs. 2–4) that did not figure in a recent survey of this site (Felton & Judd 1997): *Hypselistes jacksoni* (O.P.-Cambridge 1902), *Gonatium rubens* (Blackwall 1833) and *Savignya frontata* Blackwall 1833. The males of these species have characteristic carapace profiles, and the first is a mire indicator species. Other linyphiid carapaces were identifiable as species present in the modern fauna (Figs. 5 & 7).

The majority of the remaining carapaces were probably from female linyphiids. Although well preserved, and several seemed conspecific, they could not be positively identified from the reference collection (one is shown in Fig. 6). Leg segments were generally not kept as they were relatively lacking in useful features, but one with some possibility of identification is shown (Fig. 19).

Unequivocal identifications were also possible with the epigynum from *Pardosa pullata* (Clerck 1757) (Lycosidae) (Fig. 13), the male palpal tibia from *Erigone atra* Blackwall 1833 (Linyphiidae) (Fig. 12) and the chelicerae from *Trochosa terricola* Thorell 1856 (Lycosidae) (Fig. 15) and *Drassodes cupreus* (Blackwall 1834) (Gnaphosidae) (Fig. 16). A presumptive identification was possible for several others (Figs. 5, 8–11, 17), assuming that they were species represented in the modern fauna. The bulk of the chelicerae could be



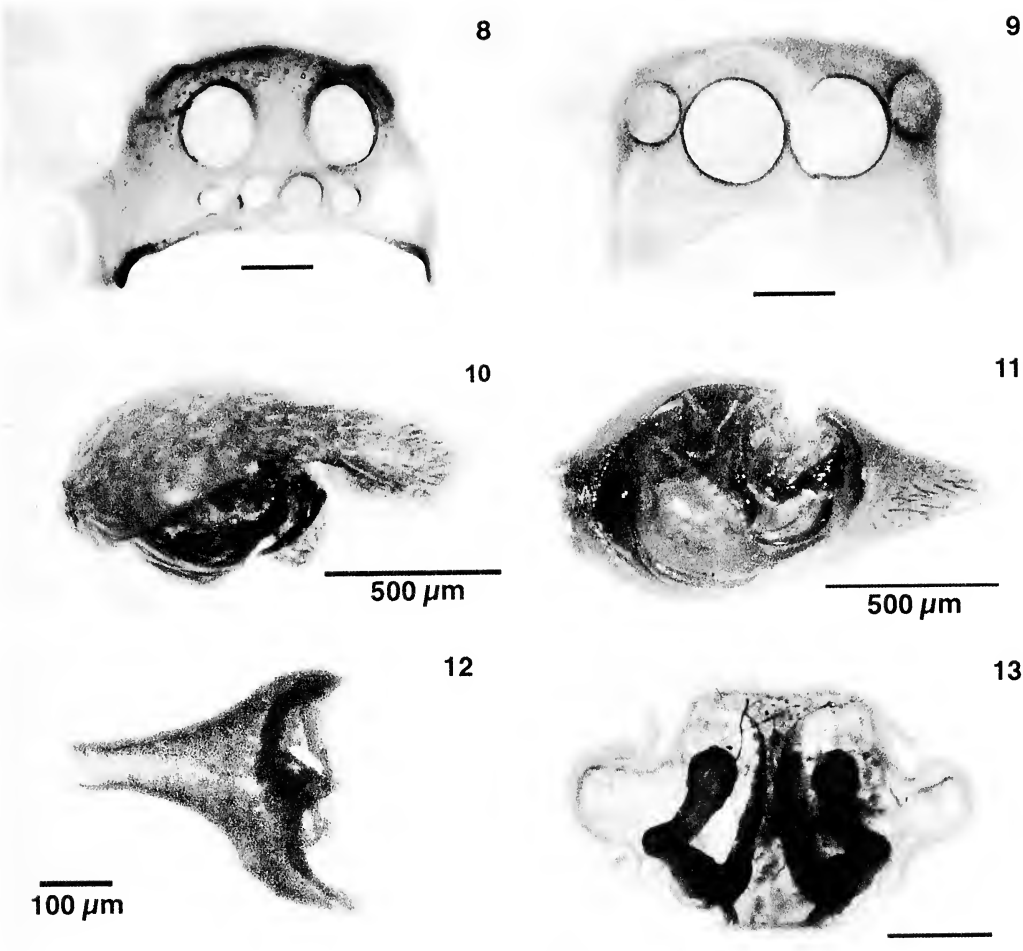
Figures 2–7.—Carapace profiles of sub-fossil linyphiids from peat at Wybunbury Moss level 1: 2. *Hypselistes jacksoni*; 3. *Gonatium rubens*; 4. *Savignya frontata*; 5. *Cnephalocotes obscurus*; 6. Unidentified (see text); 7. *Pocadicnemis pumila*. Scale bars = 200μm.

identified as from the genera *Pardosa* and *Pirata* (Fig. 14), but the cheliceral dentition of these genera is very similar.

DISCUSSION

The retrieval of identifiable spider sub-fossils exceeded initial expectations but much larger samples would need to be processed to give a useful guide to ancient faunas. Many of the mire indicator species contribute less than 1% of the total individuals in the epigeic spider fauna, as judged by present-day pitfall trapping (pers. obs.). There are few references in the literature on the retrieval of spider sub-fossils. Coope (1968), during a study of a sub-fossil insect fauna, encountered 127 spider 'cephalothoraxes' from the processing of 168 kg of organic silt from an exposed terrace in a gravel pit dated to ca. 29,000 yr. BP. These were presumably similar to the carapaces recovered in the present study, but identification to species was not attempted. Girling (1976, 1977, 1978, 1980, 1982), in a series of studies of the insect fauna from excavations of late Neolithic settlements in southwest England dated to ca. 5200 yr. BP, recovered 151 spider sub-fossils from about 400 kg of fen peat. Only one species, *Harpactea hombergi* (Scopoli 1763) (Dysderidae), was identified from these studies, on the basis of eye pattern. This species may have arrived under the bark of the timber used in the construction of the prehistoric trackways. In a later study (Girling 1984) for which quantitative data were not given, fragments of *Dolomedes fimbriatus* (Clerck 1757) (Pisauridae) and *Argyroneta aquatica* (Clerck 1757) (Cybaeidae) were identified.

Although not a primary taxonomic feature, cheliceral dentition was thought to be of tax-

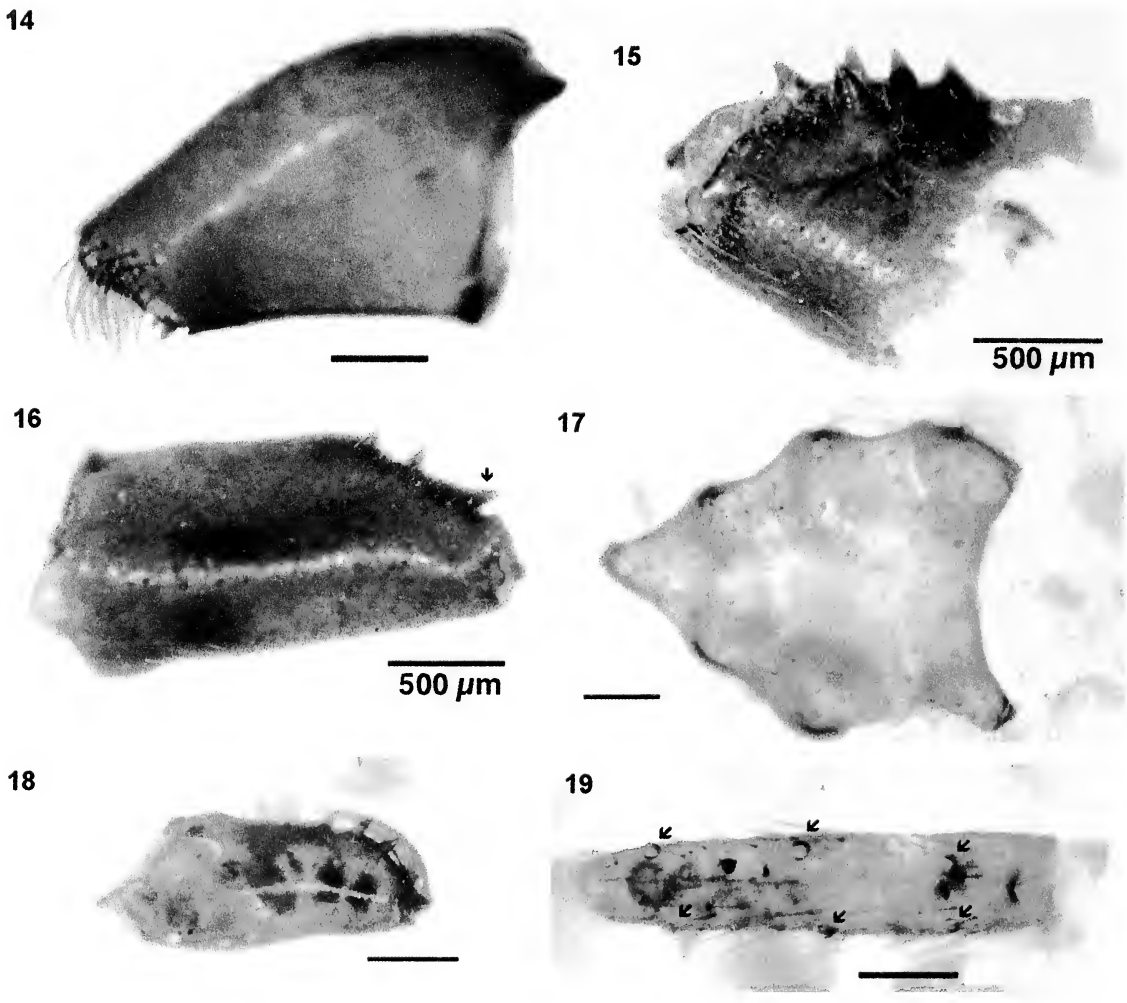


Figures 8–13.—Miscellaneous sub-fossils from peat at Wybunbury Moss: 8. Face of lycosid, possibly *Pirata piraticus*: 9. Face of salticid, possibly *Neon reticulatus*; 10. Male palp similar to *Trochosa terricola*; 11. Male palp similar to *Alopecosa pulverulenta*; 12. Palpal tibia from *Erigone atra* (level 3); 13. Epigynum from *Pardosa pullata*. All from level 1 unless indicated otherwise. Unlabelled scale bars = 200μm.

onomic value by Foelix (1982) and is used to assist in the identification of species in some genera e.g. *Tetragnatha* (see Locket & Millidge 1953). Because spider chelicerae were found to be a regular feature in extracts from peat cores, it might be possible to identify many of them to species by comparison with specimens from an appropriate reference collection. Sub-fossils of molted cuticle would exhibit the features of immature or sub-adult specimens and not relate to the adult morphology, but after study of this material it was evident that most of the sub-fossil material was from adult individuals.

It is doubtful if the species identified from sub-fossils represent their relative abundance in the cursorial fauna at the time of preservation. There may be a bias towards species that live, or build retreats, within the sphagnum layer. A large proportion of the sub-fossils will remain unidentified for lack of distinctive features. In view of these limitations, and the current lack of knowledge of their micro-habitat preferences, it seems that sub-fossil spider fragments would be rarely useful for paleoecological studies, although in the study of Girling (1984) two of the species identified were diagnostic for a fen habitat with open water.

The fact that several species were identified in this small study, goes some way to satisfy the criteria of Foster (1987) who regarded the



Figures 14–19.—Miscellaneous sub-fossils from Wybunbury Moss, level 1: 14. Chelicera from lycosid, probably *Pirata* sp.; 15. Chelicera from *Trochosa terricola*; 16. Chelicera from *Drassodes cupreus*, characteristic conical tooth arrowed; 17. Sternal plate with pigmentation adjacent to coxal articulations, similar to that of *Pirata* sp.; 18. Unidentified chelicera with fang attached: 19. Leg segment with three pairs of spine bases (arrowed). Unlabelled scale bars = 200μm.

availability of post-glacial sub-fossils as one of ten necessary attributes for any invertebrate group being used as an ecological indicator and suggests that the technique might be useful for tracing the history of individual species in the current fauna.

A higher proportion of the material might be identifiable to species if the morphology of chelicerae, sternums and carapaces of the species relevant to bogs was better known. This is complicated by the fact that some features of cheliceral dentition are not constant and that there is sexual dimorphism.

It would be informative to attempt sub-fossil retrieval from greater depth, perhaps to the sedge peats and organic muds that mark the earliest phase of mire development in post-glacial kettle-holes. The sub-fossil spider fauna of raised mires should also be investigated while a few examples of this biome still survive, without major anthropogenic modification or destruction, throughout the Holarctic temperate and boreal regions. It has to be borne in mind that a large volume of peat will need to be processed to provide sufficient material to form the basis of an ecological study.

This might be more easily obtained from exposed profiles in bogs that are being mined commercially.

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HAWAIIAN SPIDERS OF THE GENUS *TETRAGNATHA* (ARANEAE, TETRAGNATHIDAE): V. ELONGATE WEB-BUILDERS FROM OAHU

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ABSTRACT. This study continues documentation of the adaptive radiation of species in the genus *Tetragnatha* in the Hawaiian archipelago. The four new species described here are similar in gross appearance, all being brown and elongate. They all build orb webs low down in shrubby vegetation, and have disjunct or abutting ranges. The new species are *T. limu*, *T. lena*, *T. palikea*, and *T. uluhe*. Different species occur in middle and high elevations, and in wet and dry habitats. Similar to other representatives of Hawaiian *Tetragnatha*, they are strictly nocturnal web-builders.

Keywords: Hawaii, *Tetragnatha*, descriptions, taxonomy

The Hawaiian Islands are well known for having numerous radiations of closely related species (Roderick & Gillespie 1998; Simon 1987; Wagner & Funk 1995). Groups of spiders that appear to have undergone extensive species radiations in the islands include *Tetragnatha* Latreille 1804 (Tetragnathidae) (Gillespie 1991, 1992; Karsch 1880; Okuma 1988; Simon 1900), *Mecaphesa* Simon 1900 (Thomisidae) (Garb 1999; Lehtinen 1993; Simon 1900; Suman 1970), *Argyrodes* Simon 1864 (Theridiidae) (Simon 1900), *Theridion* Walckenaer 1805 (Theridiidae) (Simon 1900), *Orsonwelles* Hormiga (2002) (Linyphiidae), and a lineage of jumping spiders (Salticidae) (Gillespie et al. 1998).

This paper, the fifth in a series documenting the radiation of *Tetragnatha* spiders in the archipelago, describes new species of spiders in the genus *Tetragnatha* that are confined to similar microhabitats in different habitat types on the island of Oahu, the second oldest of the currently high Hawaiian Islands. The spiders are similar in gross appearance, all being elongate and brown, and construct large orb webs low down in the shrub vegetation. In low elevation habitats, where the environment has been disturbed, these spiders are found on grassy verges, where they can sometimes be quite numerous. At high elevations, the spiders are generally found in mossy hollows close to the ground. The single species found at high elevations on Oahu is quite similar on both mountain ranges, although there are features unique to each mountain range. The allopatric distributions of taxa are shown in Figure 1.

METHODS

Characters examined.—Morphological measurements taken were the same as those described in Gillespie (1991, 1992, 1994): eye separation; cheliceral tooth pattern; form and setation of the first and third legs (I and III representing the greatest divergence in leg function); and form and pattern of the dorsum, venter, carapace, and sternum. In order to estimate variability within a taxon and determine which features best characterize a species, where possible, measurements were taken on six individuals of each sex of each species with additional observations on other individuals once diagnostic characters had been identified. Genitalia of both sexes were examined using the methods described in Gillespie (1991).

Terminology.—The terminology for the teeth on the cheliceral margins of the males is that used in previous papers (Gillespie 1991, 1992, 1994; see Okuma 1987, 1988 and Figs. 2, 3, 9, 10). Setation on femora, tibiae and metatarsi of legs I and III is denoted by: fI, fIII, tI, tIII, mI & mIII. CITR refers to the cheliceral inter-tooth ratio, the ratio of 3 lengths: (1) between distal end of male chelicerae to sl; (2) s1 to T; and (3) T to rsu1.

The majority of the specimens were col-

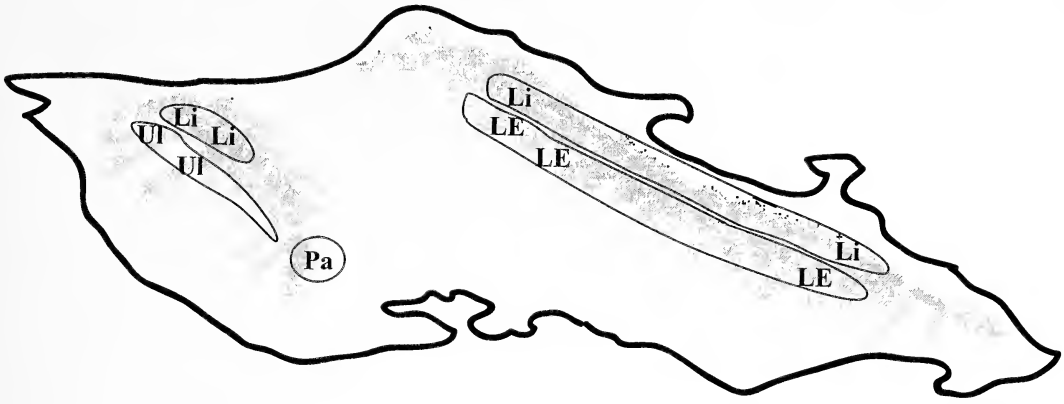
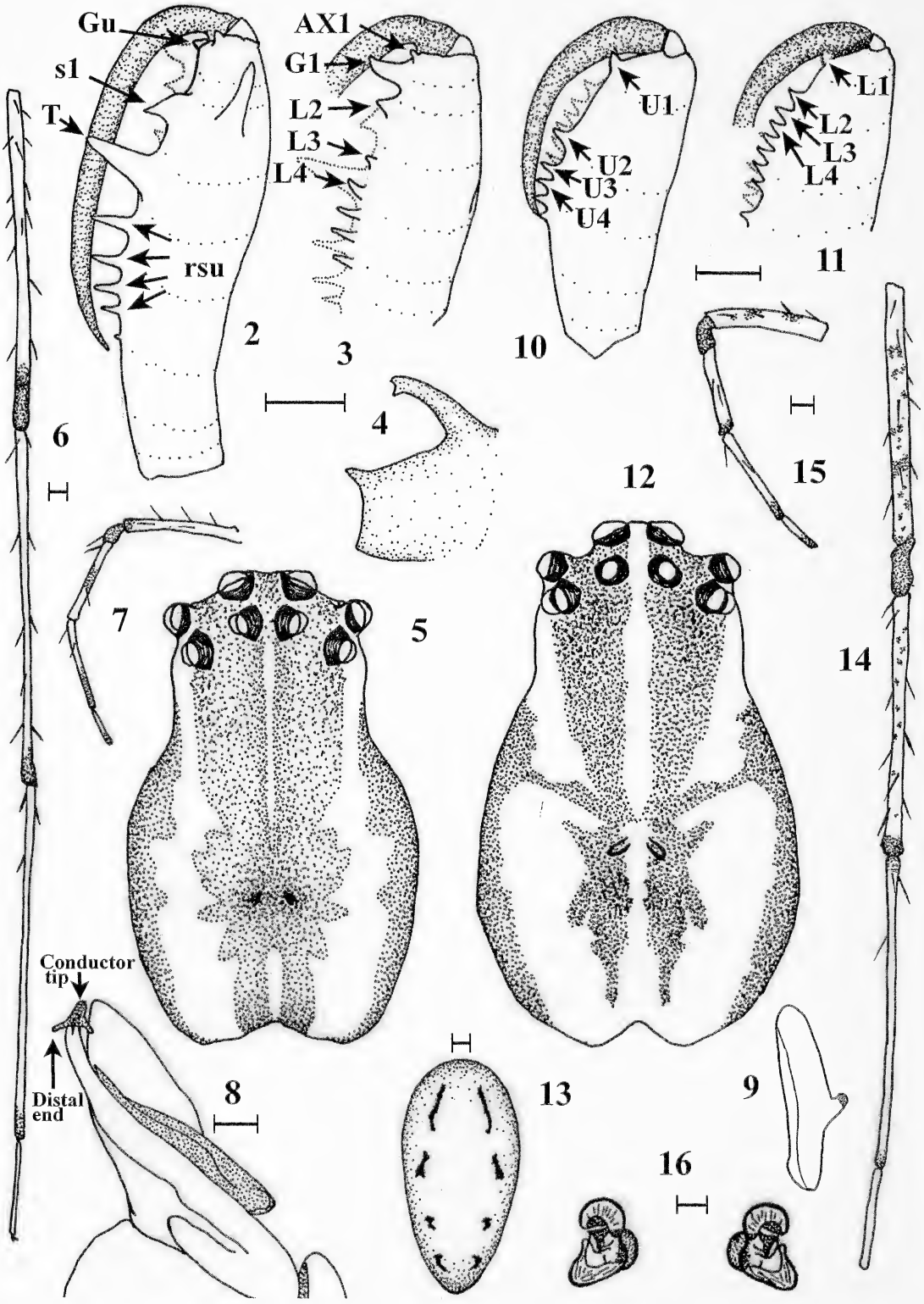


Figure 1.—Map showing allopatric distributions of elongate web-building species of Hawaiian *Tetragnatha* on Oahu. Li = *T. limu* (summits of both Waianae and Koolau mountain ranges); LE = *T. lena* (lower elevation forests of the Koolau mountains); Ul = *T. uluhe* (lower elevation/ drier forests of the Waianae mountains); and Pa = *T. palikea* (mid elevation mesic forests of the Waianae mountains).

lected by me (RGG) and George Roderick (GKR). All holotypes and allotypes have been deposited in the Bishop Museum, Honolulu (BPBM) and all paratypes will be deposited in the Essig Museum of Entomology of the University of California, Berkeley (EMUC). Unless indicated otherwise, all measurements are in mm.

KEY TO *TETRAGNATHA* SPECIES FROM OAHU

1. Lateral eyes well separated (Figs. 51, 59); chelicerae shorter than carapace ..... *Tetragnatha uluhe* new species
   Lateral eyes contiguous or almost so (Figs. 5, 12, 20, 27, 35, 43); chelicerae longer than carapace 2
2. Males 3
   Females 5
3. Backward projection of conductor well below distal projection, having appearance of Legionnaire hat (Figs. 23, 65); individuals large (9–10 mm) and robust, pale brown in life .. *Tetragnatha lena* new species
   Backward projection of conductor at same level as distal projection (Figs. 64, 66, 67); individuals usually dark-colored in life 4
4. Conductor cap broadly convex on top and constricted into a papilla at distal end (Figs. 8, 64); legs banded at distal ends of segments (Figs. 6, 7) ..... *Tetragnatha limu* new species
   Conductor drawn to point at apex and not constricted at distal end (Figs. 39, 66); legs mostly uniform in color (Figs. 37, 38) ..... *Tetragnatha palikea* new species
5. Diameters of PLEs and PMEs smaller than the distance between the PLEs (Fig. 27); cheliceral teeth large, 2nd tooth on upper cheliceral margin larger than others (Fig. 25) ..... *Tetragnatha lena* new species
   Diameters of PLEs and PMEs larger than the distance between the PLEs (Figs. 12, 43); cheliceral teeth otherwise, with 2nd tooth on upper cheliceral margin smaller than 1st tooth (Fig. 41) or similar in size (Fig. 10) 6
6. Seminal receptacles compact, separated by more than width (Fig. 16); no tubercle on distal end of upper cheliceral surface (Fig. 10) ..... *Tetragnatha limu* new species
   Seminal receptacles large, separated be less than width (Fig. 47); distinct tubercle on distal end of upper cheliceral surface (Fig. 41) ..... *Tetragnatha palikea* new species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Conductor tip
Distal end
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Tetragnatha limu new species
(Figs. 2–16, 64)

Types.—Holotype male from Oahu, Mt. Kaala 1220 m, 21.511°N, 158.145°W, RGG, 12 August 1991 (BPBM); allotype female from Oahu, Mt. Kaala 1220 m, 21.511°N, 158.145°W, RGG, 29 April 1990 (BPBM). Paratypes (EMUC): Oahu, Waianae Mountains: Mt Kaala: 1220 m, 21.511°N, 158.145°W, 16 August 1988, RGG, 1 male; 29 April 1990, 1 ♀; 12 August 1991, 1 ♂; Pahole (Peacock Flats) 600 m, 21.548°N, 158.187°W, RGG, 18 August 1988; Oahu, Koolau Mountains: Konahuanui 1030 m, 21.356°N, 157.791°W, RGG, 22 September 1990, 2 ♂; Poamoho 800 m, 21.547°N, 157.924°W, RGG, 10 April 1999.

Etymology.—The specific epithet, regarded as a noun in apposition, is the Hawaiian word for "moss" or "lichen" and refers to the microhabitat in which this species generally occurs.

Diagnosis.—*Tetragnatha limu* can be distinguished from other species based on the contiguity and relatively large size of the lateral eyes (Figs. 5, 12), the convex shape of the male conductor with a constriction at the distal end (Figs. 8, 64), and the compact shape and separation of the female seminal receptacles (Fig. 16).

Description.—*Holotype male* (Figs. 2–9, 64): Length of carapace 2.9, total length 8.0. Chelicerae 96% length of carapace. Cheliceral fang slightly shorter than base, bent over at both proximal and distal ends. Promargin of chelicerae (Fig. 2): distance between Gu and s1 slightly greater than between s1 and T, CITR approx. 0.4:0.3:0.3; Gu distinct; s1 broad hook, width about equal to length (approximately equal width and 35% height of T); T large, pointing straight out from margin of chelicerae; rsu 5 straight spikes, decreasing in size. Retromargin of chelicerae (Fig. 3): total of 7 teeth; AX1 distinct; G1 large and pointing straight out, L2–L7 showing slight increase in size proximally until second to last tooth. Dorsal spur quite long, bent (24% length of carapace); tip bifurcated (Fig. 4). Thoracic fovea distinctly marked around depression (Fig. 5). Coloration and eye pattern as in female. Leg setation similar to female (Figs. 6, 7). Conductor (Figs. 8, 64): conductor cap broad at base with flange projecting behind cap, and highly peaked. Paracymbium mitten-shaped (Fig. 9).

Allotype female (Figs. 10–16): Length of carapace 3.3, total length 9.5. Chelicerae 73% length of carapace. Cheliceral fang slightly greater than half length of base, tapering to smooth point distally. Promargin of chelicerae (Fig. 10): 6 teeth, U1 prominent, as wide but shorter than U2 and well separated (28% cheliceral length) from U2; U2 taller than other teeth; U3-U5 decreasing in size proximally. Retromargin of chelicerae (Fig. 11): series of 8 teeth: L1 approximately same size as U1, similar in size and quite well separated from L2. Remaining retromarginal teeth approximately similar in size. Eyes larger than distance separating them. Median ocular area square (Fig. 12); lateral eyes contiguous. Carapace brown with very pronounced markings including dark margins, and pair of dark lines running from behind PLE's and converging broadly towards fovea; sternum dusky. Abdomen elongate oval; dorsum brown with discrete paired markings down sides (Fig. 13); venter speckled silver with brown medial, longitudinal bar. Legs with dark spots below most spines and at distal margins of joints (Figs. 14, 15). Leg spines short and robust; setation: fI 2/3/5; tI 3/2/3; mI 1/1/1; fIII with 2 dorsal, 1 prolateral and no ventral, and tIII and mIII each with 1 prolateral, macrosetae. Seminal receptacles (Fig. 16): oval anterior bulb; angular and slightly larger posterior bulb.

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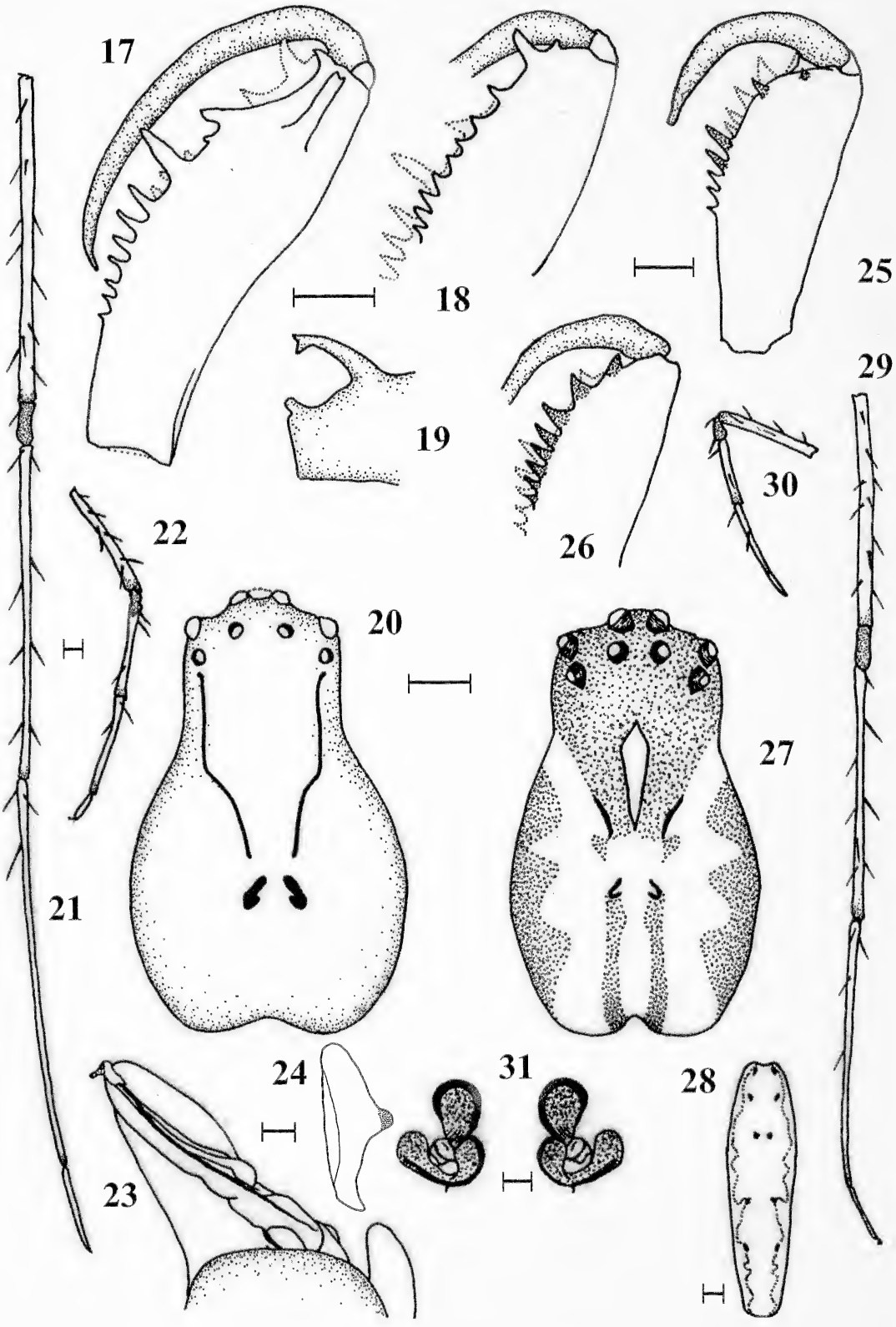
Figures 2–16.—*Tetragnatha limu*; Male. 2. Promargin of right chelicera; 3. Retromargin of left chelicera; 4. Dorsal spur of right chelicera, lateral view; 5. Carapace, dorsal; 6. Right leg I, dorsal; 7. Right leg III, prolateral; 8. Distal end of left palpus. 9. Left paracymbium. Female allotype. 10. Promargin of right chelicera; 11. Retromargin of left chelicera; 12. Carapace, dorsal; 13. Abdomen, dorsal; 14. Right leg I, dorsal; 15. Right leg III, prolateral; 16. Seminal receptacles, ventral. Scale bars = 0.5 for all except Figs. 8, 9 & 16, for which scale bars = 0.1. Scale bar between at Fig. 16 applies to Figs. 9 & 16; that between Figs. 2 & 4 applies to Figs. 2, 3, 4, 5 & 12; that between Figs. 10 & 11 applies to Figs. 10 & 11; that at Fig. 6 applies to Figs. 6 & 7; that at Fig. 15 applies to Figs. 14 & 15.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Variation.—(n = 6 ♂, 6 ♀).—Male: Carapace 2.9–3.3. CITR little variation, 0.4:0.3: 0.3; rsu usually 5, sometimes 4. Tip of dorsal spur can be more indented. Female: Length of carapace 3.2–3.6. Color patterns vary slightly; no polymorphism.

Natural history.—*Tetragnatha limu* is found mostly in wet and cloud forest on the summits of the Waianae and Koolau mountain ranges of Oahu. In the Koolaus it has been found along the summit ridge (800–1030 m); in the Waianaes it has been found on the summit of Mt. Kaala, and (very rarely) lower down to 600 m in Pahole. They are mostly found at night in webs, spun deep in the moss and lichen layer that covers the base of shrubs in the dwarf cloud forest.

Tetragnatha lena new species
(Figs. 17–31, 65)

Types.—Holotype male, allotype female from Oahu, Pua Ohia Trail 500 m, RGG, 13 April 1990 (BPBM). Paratypes (EMUC): Oahu, Koolau Mountains: Pua Ohia Trail (Tantalus) 500 m, 21.336°N, 158.158°W, W.D. Perriera, 23 July 1989, 1 ♂ RGG, 13 April 1990, 1 ♂, 3 ♀; Schofield-Waikane 630 m, 21.514°N, 157.933°W, RGG, 30 September 1989, 1 ♂; Poamoho 600 m, 21.537°N, 157.974°W, RGG, 10 April 1999.

Etymology.—The specific epithet, regarded as a noun in apposition, is the Hawaiian word for "yellowish", and refers to the light yellowish brown color of this spider.

Diagnosis.—*Tetragnatha lena* can be distinguished from other species based the small size and contiguity of the lateral eyes (Figs. 20, 27), and the shape of the male conductor (form of Legionnaire's hat) (Figs. 23, 65).

Description.—*Holotype male* (Figs. 17–24, 65): Length of carapace 3.4, total length 9.6. Chelicerae 80% length of carapace. Cheliceral fang shorter than base, bent over at both proximal and distal ends. Promargin of chelicerae (Fig. 17): distance between Gu and s1 greater than between s1 and T, CITR approx. 0.5:0.3: 0.2; Gu distinct hook; s1 angled straight down and out, narrower than long (narrower and 80% height of T); T large, pointing straight out from margin of chelicerae; rsu 7 straight spikes, decreasing in size. Retromargin of chelicerae (Fig. 18): total of 9 teeth; AX1 distinct nipple-shape; G1 large and pointing straight out, L2–L9 similar in size. Dorsal spur quite long, bent (20% length of carapace); tip bifurcated (Fig. 19). Thoracic fovea discretely marked around depression (Fig. 20). Coloration and eye pattern as in female. Leg setation similar to female (Figs. 21, 22). Conductor (Fig. 23, 65): conductor cap broad at base with broad, long flange projecting behind cap. Paracymbium with lateral notch approximately at midline, projecting out (Fig. 24).

Allotype female (Figs. 25–31): Length of carapace 3.5, total length 10.0. Chelicerae 70% length of carapace. Cheliceral fang slightly greater than half length of base, tapering to smooth point distally. Promargin of chelicerae (Fig. 25): 7 teeth, U1 small and inconspicuous, separation between U2 and U3 greater than between U1 and U2; U3 taller than other teeth; U3–U5 decreasing in size proximally. Retromargin of chelicerae (Fig. 26): series of 8 teeth: L1 much larger than U1, similar in size and close to L2. Remaining retromarginal teeth decreasing in size proximally. Eyes smaller than distance separating them. Median ocular area slightly wider posteriorly (Fig. 27); lateral eyes loosely contiguous. Carapace light brown with slightly darker markings including dark margins and pair of dark lines running from behind PLE's and converging broadly towards fovea. Abdomen elongate; dorsum pale fawn with discrete brown paired markings down sides (Fig. 28); venter speckled silver along midline with pair

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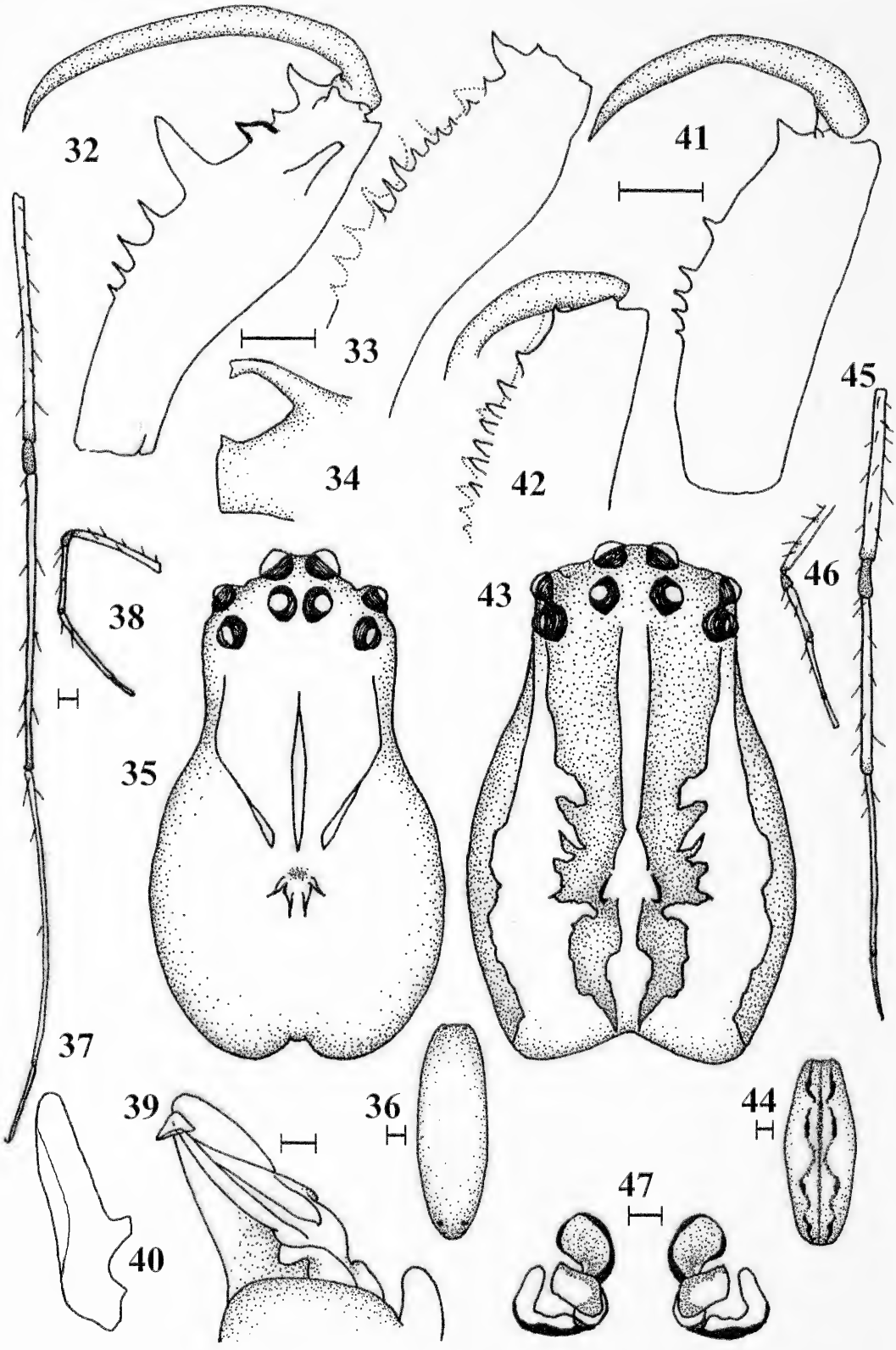
Figures 17–31.—*Tetragnatha lena*; Male. 17. Promargin of right chelicera; 18. Retromargin of left chelicera; 19. Dorsal spur of right chelicera, lateral view; 20. carapace, dorsal; 21. Right leg I, dorsal; 22. Right leg III, prolateral; 23. Distal end of left palpus; 24. Left paracymbium. Female allotype. 25. Promargin of right chelicera; 26. Retromargin of left chelicera; 27. Carapace, dorsal; 28. Abdomen, dorsal; 29. Right leg I, dorsal; 30. Right leg III, prolateral; 31. Seminal receptacles, ventral. Scale bars = 0.5 for all except Figs. 23, 24 & 31, for which scale bars = 0.1; scale bar between Figs. 23 & 24 applies to Figs. 23 & 24; that between Figs. 17 & 18 applies to Figs. 17, 18 & 19; that between Figs. 20 & 27 applies to Figs. 20 & 27; that between Figs. 21 & 22 applies to Figs. 21, 22, 29 & 30.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of brown longitudinal bars on sides. Legs pale brown. Leg macrosetae short and robust; setation: fI 3/4/3; tI 3/2/3; mI 2/1/1; fIII with 3 dorsal, 2 prolateral and no ventral, tIII with 1 dorsal, 1 prolateral, and mIII with 2 dorsal and 1 prolateral, macrosetae (Figs. 29, 30). Seminal receptacles (Fig. 31): large, oval anterior bulb; smaller, oval posterior bulb.

Variation.—(n = 6 ♂, 6 ♀).—Male: Carapace 3.1–3.4. CITR little variation, 0.5:0.3:0.2; rsu 5–7. Degree of indentation of tip of dorsal spur can vary. Female: Length of carapace 3.5–4.0. Color patterns vary slightly; no polymorphism.

Natural history.—*Tetragnatha lena* is found in middle elevation (500–700 m) mesic forest in the Koolau mountains of Oahu. It is exclusively nocturnal, and builds large orb webs at night. Because it occurs at relatively low elevations, it is often found associated with secondary growth native vegetation and alien grasses.

Tetragnatha palikea new species
(Figs. 32–47, 66)

Types.—Holotype male, allotype female from Oahu, Palikea (Honouliuli) Trail 930 m, 21.417°N, 158.103°W, RGG, 18 February 1990 (BPBM). Paratypes (EMUC): Oahu, Waianae Mountains: Palikea 930 m, 21.417°N, 158.103°W, RGG, 18 February 1990, 1 ♀, 2 ♂; 920 m, 21.416°N, 158.102°W, RGG, 12 April 1999, 1 ♂, 3 ♀.

Etymology.—The specific epithet, regarded as a noun in apposition, refers to the area (Palikea) in which this spider is found. It is part of the Nature Conservancy of Hawaii's Honoluliuli Preserve (3,692 acres) on the southeast slope of the Waianae Mountains.

Diagnosis.—*Tetragnatha palikea* can be distinguished from other species based the contiguity and relatively large size of the lateral eyes (Figs. 35, 43), the convex shape of the male conductor with no distal constriction (Figs. 39, 66) and the shape of the female seminal receptacles (close, bulbs angular, Fig. 47).

Description.— *Holotype male* (Figs. 32–40, 66): Length of carapace 2.9, total length 8.8. Chelicerae 87% length of carapace. Cheliceral fang shorter than base, bent over at both proximal and distal ends. Promargin of chelicerae (Fig. 32): distance between Gu and s1 slightly greater than between s1 and T, CITR approx. 0.4:0.3:0.3; Gu distinct; s1 broad hook, width slightly greater than length (approximately equal width and 35% height of T); T large, pointing straight out from margin of chelicerae; rsu 4 straight spikes, decreasing in size proximally. Retromargin of chelicerae (Fig. 33): total of 10 teeth; AX1 distinct; G1 large and pointing almost straight out, L2–L7 small, similar in size, L8–L10 large, similar in size. Dorsal spur quite long, bent (24% length of carapace); tip bifurcated (Fig. 34). Thoracic fovea distinctly marked around depression (Fig. 35). Abdomen similar to female but duller in color (Fig. 36). Eye pattern as in female. Leg setation similar to female (Figs. 37, 38). Conductor (Figs. 39, 66): conductor cap broad and flat at base with flange projecting behind cap, not highly peaked. Paracymbium with lateral notch below midline, angular, projecting out (Fig. 40).

Allotype female (Figs. 41–47): Length of carapace 3.0, total length 8.9. Chelicerae 75% length of carapace. Cheliceral fang slightly greater than half length of base, tapering to smooth point distally. Promargin of chelicerae (Fig. 41): small tubercle at apex; 6 teeth, U1 prominent, wider and higher than U2 and well separated (31% cheliceral length) from U2; U2–U5 decreasing in size proximally. Retromargin of chelicerae (Fig. 42): series of 8 teeth: L1 smaller than U1, similar in size and quite well separated from L2. Remaining re-

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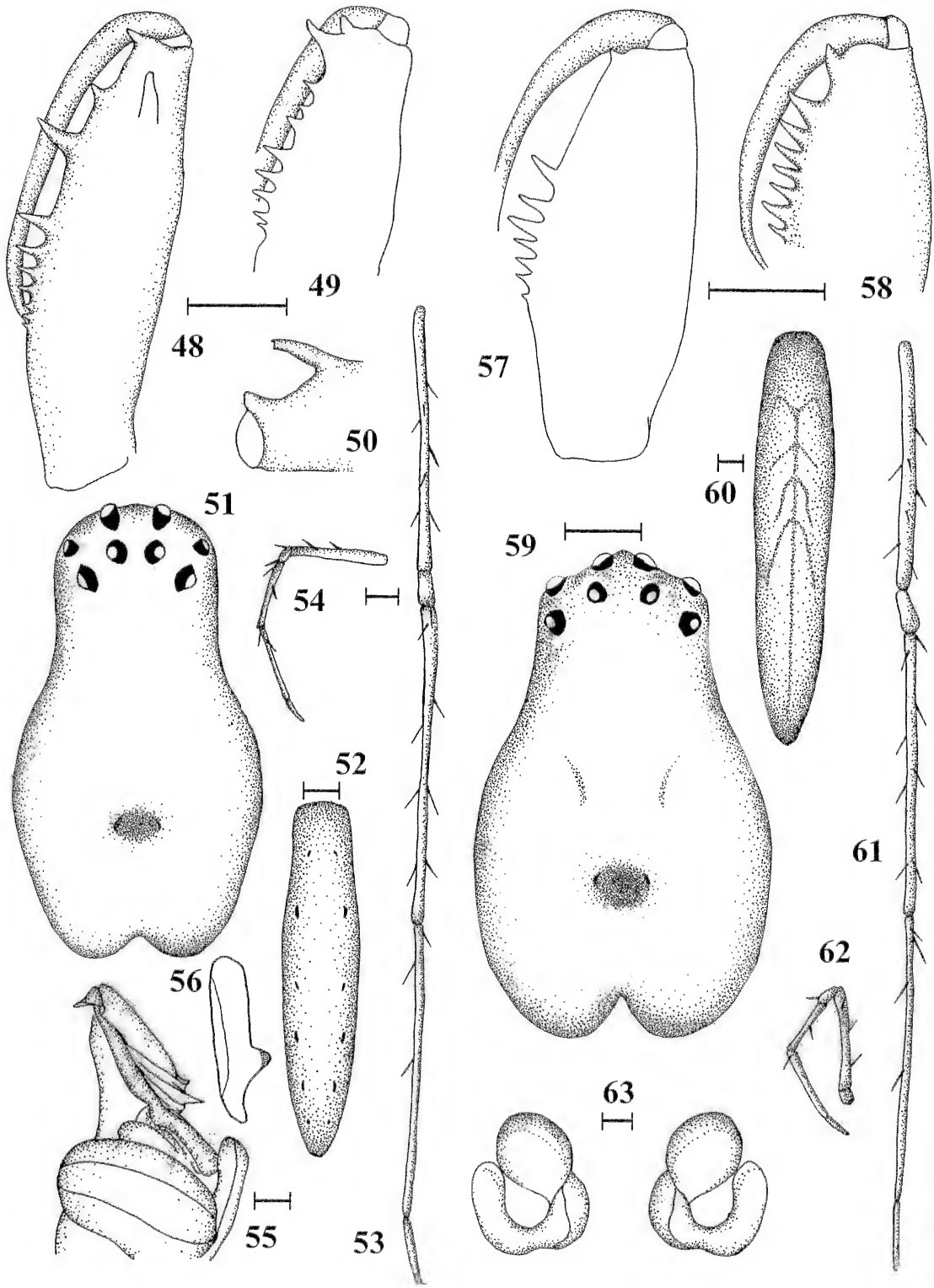
Figures 32–47.—*Tetragnatha palikea*; Male. 32. Promargin of right chelicera; 33. Retromargin of left chelicera; 34. Dorsal spur of right chelicera, lateral view; 35. Carapace, dorsal; 36. Abdomen, dorsal; 37. Right leg I, dorsal; 38. Right leg III, prolateral; 39. Distal end of left palpus; 40. Left paracymbium. Female allotype. 41. Promargin of right chelicera; 42. Retromargin of left chelicera; 43. Carapace, dorsal; 44. Abdomen, dorsal; 45. Right leg I, dorsal; 46. Right leg III, prolateral; 47. Seminal receptacles, ventral. Scale bars = 0.5 for all except Figs. 39, 40 & 47, for which scale bars = 0.1; scale bar between Figs. 32 & 33 applies to Figs. 32–35; that between Figs. 37 and 38 applies to Figs. 37, 38, 45 and 46; that at Fig. 41 applies to Figs. 41–43.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tromarginal teeth slightly larger. Eyes larger than distance separating them. Median ocular area square (Fig. 43); lateral eyes contiguous. Carapace brown with very pronounced markings including dark margins, and pair of dark lines running from behind PLE's and converging broadly towards fovea; sternum dusky. Abdomen elongate oval; dorsum brown with discrete paired markings down sides (Figs. 44). Legs with small dark spots below many spines (Figs. 45, 46). Leg macrosetae short and robust; setation: fI 3/4/5; tI 3/2/3; mI 1/1/1; fIII with 2 dorsal, 1 prolateral and no ventral, and tIII and mIII each with 1 dorsal and 1 prolateral, macrosetae. Seminal receptacles (Fig. 47): large, oval anterior bulb; narrow, angular and smaller posterior bulb.

Variation.—(n = 6 ♂, 6 ♀).—Male: Carapace 2.6–3.1. CITR little variation, 0.4:0.3:0.3; rsu usually 4. Female: Length of carapace 2.9–3.2. Color patterns vary slightly; no polymorphism.

Natural history.—*Tetragnatha palikea* is found mostly in webs built over the leaf litter, or low in the vegetation, on the south end of the Waianae mountain range of Oahu.

Tetragnatha uluhe new species
(Figs. 48–63, 67)

Types.—Holotype male from Halona Valley, 460 m, 21.427°N, 158.159°W, D.J. Preston, 31 January 1996 (BPBM); allotype female from Pahole, 550 m, 21.552°N, 158.199°W, T. Blackledge and RGG, 19 August 2000 (BPBM). Paratypes (EMUC): Oahu, Waianae Mountains: Halona Valley, 460 m, D.J. Preston, 31 January 1996, 1 ♂; Waianae Kai, 550 m, 21.508°N, 158.170°W, RGG & GKR, 2 March 1999, 1 ♂; Pahole, 550 m, 21.552°N, 158.199°W, RGG, GKR, T. Blackledge, 19 August 2000, 2 ♀, 1 ♂.

Etymology.—The specific epithet, regarded as a noun in apposition, is the Hawaiian word for false staghorn fern (*Dicranopteris*), a native species most abundant in second growth and mesic forest. This is where the spider is most commonly found.

Diagnosis.—*Tetragnatha uluhe* cannot easily be confused with other species as its eye configuration (lateral eyes well separated) is very distinctive (Figs. 51, 59).

Description.—*Holotype male* (Figs. 48–56, 67): Length of carapace 3.0, total length 8.0. Chelicerae 75% length of carapace. Cheliceral fang slightly shorter than base, bent over at both proximal and distal ends. Promargin of chelicerae (Fig. 48): distance between Gu and s1 similar to that between s1 and T, CITR approx. 0.33:0.33:0.33; Gu and sl both distinct but small, similar in size (sl narrower and 30% height of T); T large, pointing slightly up and out from margin of chelicerae; rsu 7 straight spikes, decreasing in size proximally. Retromargin of chelicerae (Fig. 49): total of 10 teeth; AX1 large point; G1 very large, pointing slightly up and out, L2–L4 small, similar in size; L5–L7 larger, and L8–L9 smaller. Dorsal spur quite long, curved over (32% length of carapace); tip slightly bifurcated (Fig. 50). Thoracic fovea distinctly marked around depression (Fig. 51). Coloration and eye pattern as in female. Abdomen similar to female but plain (Fig. 52). Leg setation similar to female (Figs. 53–54). Conductor (Figs. 55, 67): conductor cap pointed out, with minimal flange projecting behind cap, and not highly peaked. Paracymbium with lateral notch below midline, projecting out (Fig. 56).

Allotype female (Figs. 57–63): Length of carapace 3.1, total length 11.2. Chelicerae 58% length of carapace. Cheliceral fang slightly greater than half length of base, tapering to smooth point distally. Promargin of chelicerae (Fig. 57): 8 teeth, U1 prominent,

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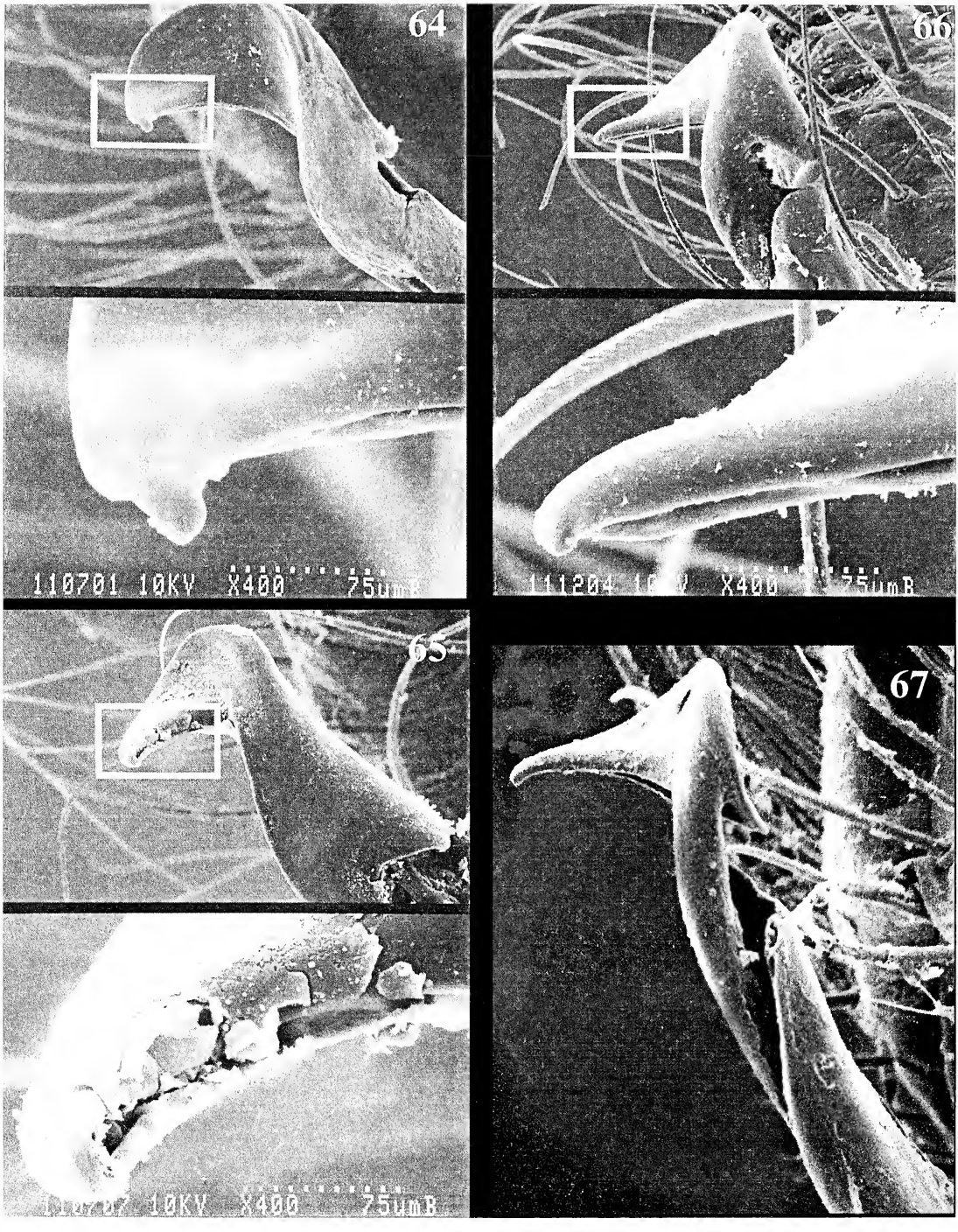
Figures 48–63.—*Tetragnatha uluhe*; Male. 48. Promargin of right chelicera; 49. Retromargin of left chelicera; 50. Dorsal spur of right chelicera, lateral view; 51. Carapace, dorsal; 52. Abdomen, dorsal; 53. Right leg I, dorsal; 54. Right leg III, prolateral; 55. Distal end of left palpus; 56. Left paracymbium. Female allotype. 57. Promargin of right chelicera; 58. Retromargin of left chelicera; 59. Carapace, dorsal; 60. Abdomen, dorsal; 61. Right leg I, dorsal; 62. Right leg III, prolateral; 63. Seminal receptacles, ventral. Scale bars = 0.5 for all except Figs. 55, 56 & 63, for which scale bars = 0.1; scale bar between at Fig. 55 applies to Figs. 55 & 56; that between Figs. 48 & 49 applies to Figs. 48–50; that at Fig. 59 applies to Figs. 51 & 59; that between Figs. 53 & 54 applies to Figs. 53, 54, 61 & 62; that between Figs. 57 & 58 applies to Figs. 57 & 58.



Figures 64–67.—Scanning electron micrographs of conductor of male palps. 64. *T. limu*; 65. *T. lena*; 66. *T. palikea*; 67. *T. uluhe*.

small, much smaller than U2 and well separated (33% cheliceral length) from U2; U2–U4 large, U5-U8 decreasing in size proximally. Retromargin of chelicerae (Fig. 58): series of 8 teeth: L1 than U1, smaller and quite well separated from L2. Remaining retromarginal teeth gradually decreasing in size proximally. Diameter of eyes smaller than distances sep-

arating them. Median ocular area wider posteriorly (Fig. 59); lateral eyes well separated. Carapace brown with indistinct markings. Abdomen elongate; dorsum light brown with indistinct markings (Fig. 60). Legs without spots. Leg spines short and robust; setation: fI 2/3/3; tI 3/1/3; mI 2/1/1; fIII with 2 dorsal, 2 prolateral and no ventral, and tIII with 1 prolateral, and mIII with 1 dorsal, macrosetae (Figs. 61–62). Seminal receptacles (Fig. 63): anterior bulb almost spherical, posterior oblong, tightly coiled together.

Variation.—(*n* = 6 ♂, 2 ♀).—Male: Carapace 2.7–3.1. CITR little variation; rsu 5–7. Female: Length of carapace 2.9–3.1. Color patterns vary slightly; no polymorphism.

Natural history.—*Tetragnatha uluhe* is confined to mesic/dry forest on the west side of the Waianae mountain range of Oahu. Its distribution is interesting, because it abuts *T. limu* in the north east, and *T. palikea* in the south. However, the species have never been found to co-occur.

ACKNOWLEDGMENTS

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FIRST SPECIES OF *AUSTROPSOPILIO* (OPILIONES, CADDOIDEA, CADDIDAE) FROM SOUTH AMERICA

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ABSTRACT. The first species of the genus *Austropsopilio* is described from South America. The species, *A. sudamericanus*, closely resembles those from Australia and Tasmania but lacks the elongate ocular tubercle previously regarded as diagnostic for the genus. Problems in the taxonomy of the genus are discussed.

RESUMEN. Se reporta por primera vez la presencia del Género *Austropsopilio* para Sudamérica. La especie *A. sudamericanus*, se parece bastante a las de Australia y Tasmania, pero no posee el tubérculo ocular previamente indicado en la diagnosis del génerica. Se discute la problemática en la taxonomía del género.

Keywords: *Austropsopilio*, Opiliones, harvestman, Chile, systematics, South America, new species

Until now, the caddoid genus *Austropsopilio* Forster 1955 encompassed two described species from eastern Australia (Forster 1955; Cantrell 1980) and one from Tasmania (Hickman 1957) and at least one undescribed species from South America (Cokendolpher & Maury 1990). The type species, *A. novaehollandiae* Forster 1955, was described from a single "immature female," and differed from the other then-recognized caddoid genera, namely, *Caddo* Banks 1892, *Acropsopilio* Silvestri 1904 (syn. *Zeopsoplio* Forster 1948) and *Caddella* Hirst 1925 (syn. *Oonopsopilio* Lawrence 1931) in having an anteriorly elongated eye tubercle ending in a bilateral pair of projections and large palps in which all articles except the tarsus bear one or more large spiny apophyses. Shear (1975, 1996) argued that *Tasmanopilio* Hickman 1957 should be synonymized with *Austropsopilio* based on similarities in pedipalpal structure, but Cokendolpher & Maury (1990), citing observations of Gruber (1974), argued for the distinctness of the two genera.

Here we describe the first species of *Austropsopilio* from South America. Cokendolpher & Maury (1990) reported the presence of the genus in Valdivian rainforests of Chile and immediately adjacent regions in Argentina based on numerous immatures and one poorly preserved adult female. Given the paucity of taxonomically useful material, they chose not to describe a new species. Adult females (but no males) were collected by the junior author via Berlese extraction from Valdivian rainforests in April 2001, thereby allowing a new species to be diagnosed and described.

All specimens collected by T. Cekalovic. Abbreviations: AMNH, American Museum of Natural History, New York; UMD, J.W. Shultz, University of Maryland, College Park.

SYSTEMATICS

Austropsopilio sudamericanus
new species
Figs. 1–12

Austropsopilio sp.: Cokendolpher & Maury 1990: 61.

Type data.—Holotype: adult female, CHILE: Provincia Valdivia, Parque Oncol (39°41′S, 73°18′W), 13 April 2001, T. Cekalovic. Paratype: 1 immature, CHILE: Provincia Valdivia, Parque Oncol (39°41′S, 73°18′W), 600 m, 4 January 2002, T. Cekalovic. Holotype and paratype deposited in AMNH.

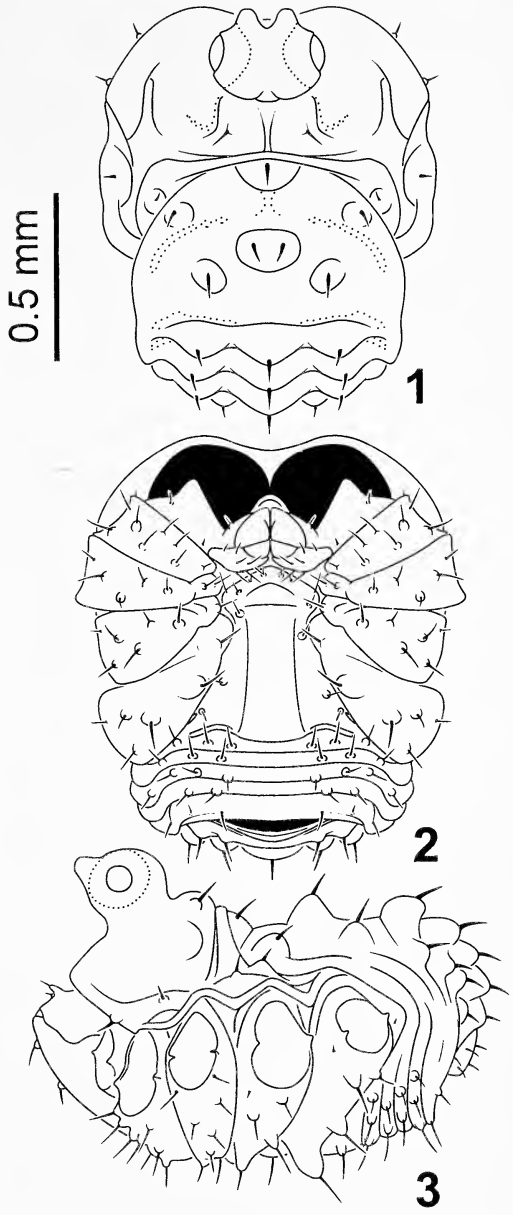
Other material (non-types).—CHILE: *Valdivia*: Parque Oncol (39°41′S, 73°18′W),

13 February 2000, 5 immatures (AMNH); 19 February 2000, 2 immatures (AMNH). Cerro Oncol (39°41′S, 73°18′W), 485 m, 15 February 2000, 1 immature (AMNH); 485 m, 13 April 2001, 10 females (UMD); 485 m, 13 April 2001, 2 ♀(AMNH); 700 m, 14 January 2001, 2 immatures (AMNH). Sendero Calfuco (39°41′S, 73°18′W), 20 January 2001, 2 immatures (AMNH); 16 January 2001, 17 immatures (AMNH); 9 January 2001, 4 immatures (AMNH); 600m, 4 January 2002, 7 immatures (UMD). Sendero Punucapa (39°41′S, 73°18′W), 3 January 2002, 1 immature (UMD). *Chiloe*: Isla Chiloe: Pid-Pid (42°24′S, 73°47′W), 4 February 2001, 1 immature (AMNH). Estero Llicaldad (42°31′S, 73°48′W), 6 February 2001, 2 immatures (AMNH). San Antonio de Chadmo (42°58′S, 73°37′W), 8 February 2001, 6 immatures (AMNH).

Etymology.—The species is named for being the first representative of its genus discovered in South America.

Distribution.—*Austropsopilio* has been collected in the Region de los Lagos of Chile and adjacent regions of Argentina (39°–40° S. Lat.) south through the northern half of Provincia Aisen (~ 46° S. Lat.) (Cokendolpher & Maury 1990).

Diagnosis.—*Austropsopilio sudamericanus* is the first and only species of the genus known from South America; other species occur in eastern Australia and Tasmania. *A. sudamericanus* differs from all other known species in that the lenses and body of the eye tubercle do not extend beyond the anterior margin of the carapace, although the paired projections of the optic tubercle may extend to the anterior margin of the carapace. In addition, the spine-bearing prominences on the opisthosomal tergum (Figs. 1, 3) are much larger in adult female *A. sudamericanus* than in other species, although they are not enlarged in earlier instars.



Figures 1–3.—General morphology of a typical adult female *A. sudamericanus*. 1. dorsal perspective. 2. ventral perspective. 3. lateral perspective.

Description.—*Adult female*: Carapace in the form of a broad, strongly recurved crescent; posterior concavity receiving opisthosoma (Fig. 1). Posterior lateral angles of carapace embracing lateral surface of opisthosoma to level of lateral posterior margin of first opisthosomal tergite. Anterior margin of carapace with broad but shallow, median supracheliceral emargination (Figs. 1, 2). Anterior margin of carapace folds ventrally to form a triangular supracheliceral doublure that passes posteriorly, tapers and attaches to the dorsal margin of the epistome (Fig. 2). Central periocular region of propeltidium steeply elevated, separated from less elevated lateral marginal fold by a bilateral pair of large, roughly longitudinal, submarginal sigillary depressions. Propeltidium lightly colored with coat-

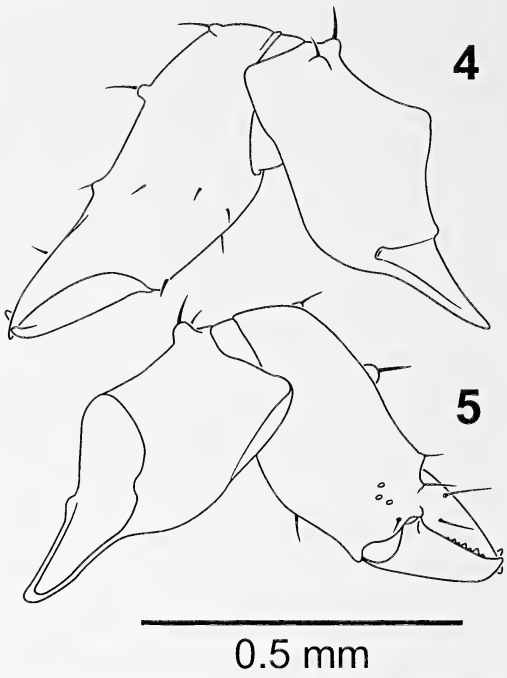
ing of small, dark denticles; denticles decrease in size and density on ocular tubercle.

Ocular tubercle large, occupying over one third the midsagittal length of the prosoma, not noticeably elongated. Ocular tubercle slightly oval in lateral perspective; wider than long in dorsal perspective, width (including lenses) about one-third maximum width of carapace. Ocular tubercle with wide, shallow midsagittal groove. Anterodorsal surface with bilateral pair of thick, blunt projections extending anterodorsally to a point approximately even with the anterior margin of the carapace.

Marginal fold weakly developed anteriorly, progressively more well developed posteriorly; scalloped in lateral perspective with three arches (Fig. 3). Arch associated with coxa II very pronounced; arch associated with coxa III less pronounced; arch associated with coxa IV with anterior half formed by marginal fold of prosoma and posterior half by lateral surface of opisthosoma. Marginal fold inflated anterior and posterior to first arch; inflated regions separated dorsally by a variably developed oblique groove. Ozopore opens within depression on lateral margin of fold just anterior to first arch. Lateral margin with three bilateral pairs of spines. First pair projecting anteroventrally at level of pedipalpal coxa, second pair projecting anterolaterally from anterior inflated region, third pair projecting dorsally from posterior inflated region.

Mesopeltidium with large postocular mound with one bilateral pair of stout spines; mound posteriorly with shallow midsagittal groove. Mesopeltidium separated from propeltidium laterally by bilateral pair of darkly colored procurved grooves which fade laterally. Cuticle with coloration and denticles like those of the propeltidium. Metapeltidium represented medially by a thin transverse fold, separated from mesopeltidium by a distinct transverse groove that fades laterally into the submarginal depressions. The metapeltidial fold expands laterally and turns abruptly posteriorly to embrace the lateral surface of the opisthosoma. Lateral portions of fold with one bilateral pair of large rounded prominences, each prominence with a recurved spine. Cuticle of metapeltidium darker than remainder of carapace and similar to opisthosoma in having dense coat of coarse, dark denticles.

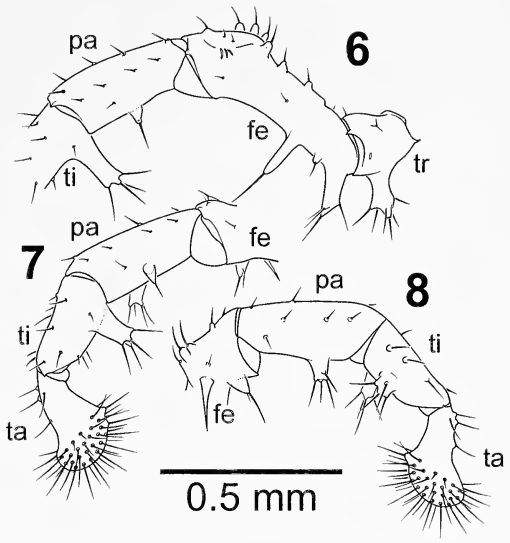
Chelicera: First article lightly colored with scattered, small dark denticles; one superior spine extending from a well-developed tubercle and a smaller, medially adjacent spine emerging from a smaller tubercle (Figs. 4, 5); a third small spine variably present. Second article lightly colored and with scattered small dark denticles, but cuticle of fixed finger and pericondylar regions dark brown. Spination of second article consisting of a superior longitudinal series of three spines, each extending from a tubercle; a loosely organized, subcircumferential row of about six small spines, beginning near the distal lateral condyle and passing medially and proximally around the article; two small spines on the base of the fixed finger; and a small spine associated with the distal medial condyle. Lateral surface with few spines compared to medial surface but with three lightly colored slit sensilla in a short longitudinal or sublongitudinal series associated with the distal lateral condyle. Fixed finger with tooth row composed of a proximal series of about six large, subequal, triangular teeth and distal series of five shorter teeth with steeply sloped proximal edges and gradually sloped distal edges. Moveable finger of chela with smooth dark cuticle. Tooth row with



Figures 4–5.—Right chelicera of typical adult female *A. sudamericanus*. 4. Medial perspective. 5. Lateral perspective.

proximal series of three or four low triangular teeth followed by a staggered series of five large and four small triangular teeth. Tip of moveable finger offset prolaterally from tooth row such that tip and ultimate tooth embrace the end of the fixed finger when chela is closed.

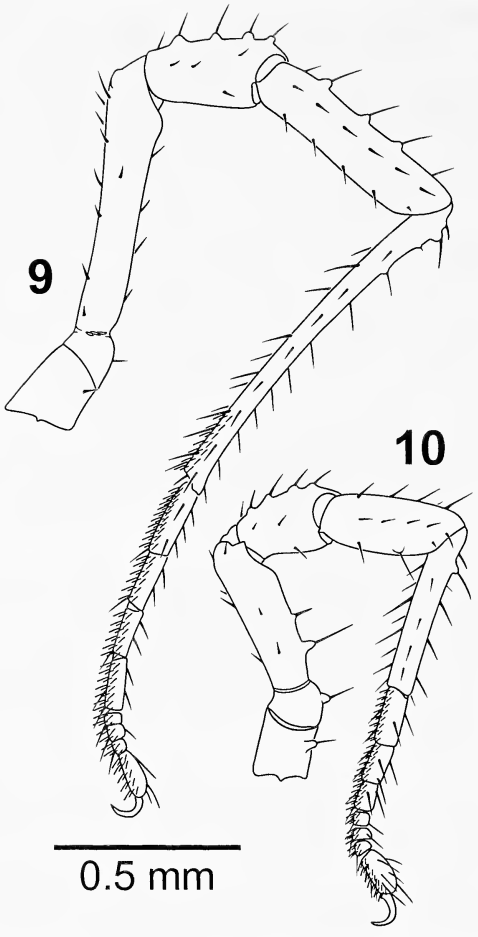
Pedipalp: Coxa: coxapophysis projecting ventrally, arranged transversely forming posterior border of stomotheca; anterior surface with soft cuticle, posterior surface with harder cuticle and with six to eight long dark setae (Fig. 2). Enditic "lips" formed by lobes of soft cuticle. Trochanter: inferior surface with large subcylindrical apophysis ending bluntly, typically bearing five or six terminal and subterminal spines. Otherwise with several small, submarginal spines (Fig. 6). Femur: proximal inferior surface with two large apophyses (Fig. 6). First inferior apophysis arising near proximal inferior margin, long, subcylindrical through most of length but with tapering terminal region ending in one spine; base of tapering region with three radially arranged evenly spaced subterminal spines. Second apophysis distally and retrolaterally adjacent to first apophysis, long, thin, slightly curved prolaterally, with one terminal spine. Small tubercle with terminal spine usually interposed between first and second inferior apophyses. Distal inferior surface (Fig. 8) with one short, tapering apophysis with one large terminal spine and one smaller subterminal spine; sometimes appearing as two basally fused apophyses of unequal length, each terminating with a single spine. Distal prolateral surface (Fig. 8) with large, tapering spike-like apophysis, terminal end very dark; in intact animal, spikelike apophyses from opposite pedipalps cross above bases of chelicerae. Middle third of superior surface with imperfect longitudinal row of three or four tubercle-based spines (Fig. 6). Distal third of superior prolateral surface with longitudinal row of three, large, closely spaced tubercle-based spines (Figs. 6, 8). Other surfaces with eight or so small scattered spines. Distal superior surface with three large, closely spaced, roughly transverse slit sensilla (Fig. 6). Patella: tapering apophysis emerging from inferior retrolateral surface, terminating in a single spine (Figs. 6, 7). Subcylindrical apophysis arising from inferior prolateral surface, terminating abruptly with "crown" of four spines (Figs. 7, 8). Superior



Figures 6–8.—Pedipalp of typical adult female *A. sudamericanus*. 6. Retrolateral surface of proximal articles. 7. Retrolateral surface of distal articles, perspective rotated slightly from that shown in 6. 8. Prolateral surface of distal articles. Abbreviations: *fe,* femur; *pa,* patella; *ta,* tarsus; *ti,* tibia; *tr,* trochanter.

surface with three imperfect rows of spines, each with three or four members. Inferior surface unarmed. Tibia: large subcylindrical apophysis projecting from distal prolateral surface and larger subcylindrical apophysis projecting from proximal retrolateral surface; both terminating in "crown" of four long, tapering, evenly spaced spines (Figs. 6–8). Superior prolateral surface with longitudinal row of three large tubercle-based spines, decreasing in size distally. Superior retrolateral surface with longitudinal row of three smaller spines. Superior surface with 0–2 small spines. Retrolateral surface with one spine arising subterminally and one arising at base of retrolateral apophysis. Inferior surface unarmed. Tarsus: inflated distally with brushlike array of about 40 spines; each spine with a dark base and translucent tip. Superior surface of thinner proximal region of tarsus with imperfect longitudinal row of three spines, proximal member of row associated with one prolateral spine and one retrolateral spine; proximal spines thus arranged in a roughly T-shaped pattern. Claw apparently absent.

Legs: Measurements of the leg segments are listed in Table 1. Coxa: inferior surface with 4–8 prominent, irregularly spaced tuber-



Figures 9–10.—Legs of typical adult female *A. sudamericanus*. 9. Leg I, right, retrolateral perspective. 10. Leg IV, right, retrolateral perspective.

cles, each with a single curved terminal spine (Figs. 2, 3). Cuticle uniform, light brown, with scattered small, dark denticles. Medial margin of coxae II–IV joining ventral body surface via lightly colored raised lobes. Inferior proximal surface of coxa IV with two, longitudinally arranged, ventrally projecting, blunt protuberances covered by sharp denticles; each protuberance ending with notably thickened spine; proximal protuberance large, more well developed than distal protuberance. Coxapophysis of leg I large, oval; fused to ventral body wall just posterior to pedipalpal coxapophyses. Coxapophysis of leg II very small. Trochanter: typically with four small spines arranged almost symmetrically near distal margin. Cuticle uniform, light brown, concolorous with coxa. Femur: shaft divided proximally by oblique circumferential groove (pseudoarticulation) forming distal border of femoral annulus; superior length of annulus shorter than inferior length (Figs. 9, 10). Annulus typically with one inferior spine, which on leg I emerges from a tubercle. Femur through telotarsus with five variably developed longitudinal rows of spines; i.e., superior (S), superior prolateral (SP), superior retrolateral (SR), inferior prolateral (IP) and inferior retrolateral (IR). Postannular shaft of femur with all spine rows. S, SP, SR present but imperfectly aligned especially distally, spines thus sometimes difficult to assign to specific rows; distal members largest, sometimes arising from tubercles. IR spines large, emerging from tubercles on leg I only. IP spines small. Cuticle of superior surface of annulus and basal part of postannular shaft lightly colored; inferior surface of annulus darker. Cuticle darkens along postannular shaft (central third appearing as dark brown band) then lightens distally. Patella: spine rows S, SP, SR present; S, SP with 4–6 members, SR with 2 or 3 members; IP, IR usually present, with one or two members. S spines arise from tubercles that tend to increase in size distally; spines in other rows lacking tubercles. Cuticle light brown proximally, lighter distally. Tibia: all spine rows present, symmetrically distributed, with four to seven members that are often regularly spaced. S spines arising from apophyses. One or two eccentric superior spines often present, especially distally. Distal one-fourth to one-fifth of inferior surface with numerous setae that increase in length distally. Cuticle of central half brown, grading into lighter brown proximally and even lighter brown distally. Basitarsus (= metatarsus): all spine rows present, symmetically arranged, typically with 5 to 12 members depending on basitarsal length; spines of S, SP, SR regularly spaced within rows. Proximal (first) member of S small, tending to be located slightly retrolateral to primary row axis; second much larger, extending from tubercle; third specialized, expressed as transverse pair of small, thin, closely spaced, erect spinules. IP, IR spines longer than those of other rows, especially distally. Cuticle light brown proximally and throughout most of length; distal one-fourth grades into distal light band. Telotarsus (= "tarsus"): formula of telotarsus: 7/9/8–9/8–9. First to penultimate articles showing regular decrease

Table 1.—Lengths of leg articles of holotype (in mm); body length = 1.2 mm, width = 0.9 mm.

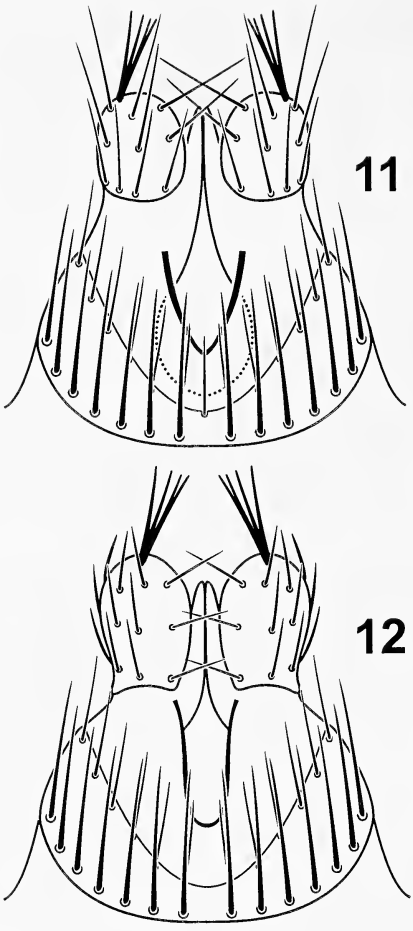
	Trochanter	Femur	Patella	Tibia	Basitarsus	Telotarsus
Leg I	0.14	0.52	0.22	0.30	0.46	0.50
Leg II	0.18	0.68	0.38	0.52	0.76	0.74
Leg III	0.14	0.54	0.32	0.36	0.66	0.68
Leg IV	0.19	0.82	0.38	0.54	1.00	0.80

in length, although antepenultimate article slightly inflated compared to adjacent articles. Ultimate article about as long as first or second article. All spine rows present. S, SP, SR spines well developed throughout telotarsus; IP, IR well developed on first two or three articles but replaced by and/or transformed into long paired setae on the distal inferior margin of each article. Inferior, prolateral and retrolateral surface with coat of short fine setae, coat of medium-length setae on inferior surface. Cuticle light brown throughout. Claw large, strongly curved.

Opisthosoma: Dorsal surface: tergite I typically with three rounded prominences, one large median prominence near anterior margin usually bearing one recurved spine (sometimes two) and one bilateral pair of smaller prominences located lateral and posterior to medial prominence, each bearing one recurved spine (Figs. 1, 3). Tergite II largest, typically with three rounded prominences; median prominence with one spine; one bilateral pair of posterolateral prominences each with one spine. Tergites III–VI short, becoming progressively shorter and more strongly recurved posteriorly, each with one row of typically 3 (sometimes 4) basally contiguous rounded prominences. Each prominence with a single recurved spine; median prominence usually slightly larger. Tergite VII platelike, posterior margin less recurved than preceeding tergites and bearing a single posterior median prominence with one terminal spine. Tergites VIII, IX and anal operculum apparently fused to form composite anal plate, although tergites may be discernable as two weakly defined rows of spines. Dorsal surface covered by dark, closely spaced denticles. Denticles less dense on tergal prominences and absent on transversely arranged, lightly colored sigillary bands that define tergal borders.

The description provided above is "typical," but there is substantial and frequent variation in the number, size and symmetry of tergal prominences, both within and between individuals. Median prominences may be divided sagittally to form two similarly or differently sized medial prominences, lateral prominences may be expressed on one side but not the other; two lateral prominences may exist on one side and one or none on the other, etc.

Ventral surface: sternite I (arculi genitales) triangular median plate with anteromedian apex; medial anterior margin abutting coxapophyses of pedipalp, lateral anterior margin abutting posterior margin of coxapophyses of leg I. Posterior lateral "corners" of triangle extend laterally as continuously narrowing strips until meeting coxapophysis of leg II, then turn posteriorly and continue along medial margins of coxae III and IV and posterior margin of coxa IV to join remaining opisthosomal cuticle. Genital sternite and operculum: genital operculum with broad, procurved posterior margin (Fig. 2). Attached lateral margins subparallel posterior to coxae, transverse width of intracoxal region gradually reduced anteriorly. Median longitudinal region raised slightly, but this ends abruptly anteriorly, as indicated by distinct transverse discontinuity at base of free lobe. Free lobe expanded posteriorly, lateral margins curve medially to meet at blunt anteromedian point. Marginal and submarginal surfaces of operculum with irregular array of about 16 to 18 tubercles each bearing one curved terminal spine; anterior margin of free lobe also with three or four bilateral pairs of simple setae. Cuticle of attached portion of operculum with numerous, closely spaced, transverse rows of small dark denticles; denticles not so organized on free lobe. Opercular cuticle translucent, revealing paired sclerotized bands of ovipositor sheath and arrays of dark setae of ovipositor (Figs. 11, 12); operculum thus appearing to have two dark longitudinal stripes and a central lighter stripe. Softer, more flex-



Figures 11–12.—Ovipositor of *A. sudamericanus*. 11. Ventral perspective. 12. Dorsal perspective.

ible lateral cuticle of genital segment lateral to operculum with regularly spaced array of small dark denticles; occasionally with one or two pairs of tubercles each bearing a spine. Stigmata located within soft lateral cuticle just posterior to coxa IV; elongated transversely; margins with line of dark cuticle. Postgenital sternites: sternites represented by six short, well-defined transverse folds separated by deep grooves. Folds fade out laterally, generally not continuous with those separating tergites. Postgenital sternites 1–5 each with single transverse row of six to eight tubercles each with one terminal spine; tubercles fewer and smaller medially. Tubercles often forming imperfect, obliquely longitudinal rows spanning several adjacent sternites, intersegmental rows begin anteromedially and end posterolaterally. Anterior margin of first postgenital sternite procurved medially, receiving posterior margin of genital operculum. Fold separating postgenital sternites 5 and 6 more weakly developed laterally than anterior counterparts, medial region typically lacking fold, sternites appearing continuous. Postgenital sternite 6 without obvious transverse divisions, suggesting consolidation of sternites from two somites (i.e., sternites of opisthosomal somites VIII and XI); posterior margin forming anterior margin of anus.

Ovipositor: Trunk with two circumferential rows of long setae (Figs. 11, 12), setae of proximal row longer and thicker than those of distal row. Ventral and dorsal surfaces with pairs of longitudinal cuticular thickenings. Paired terminal lobes each with three loosely organized "whorls" of setae; terminates in four-branched sense organ. Medial valvelike projections between lobes.

Adult male: Unknown.

Immatures: The general morphology and color patterns of immature specimens are similar to those of the adult female. In general, however, immatures are more lightly colored than adults and the spination and associated cuticular structures (i.e., tubercles, protuberances and prominen ces) are either lacking or poorly developed. The pedipalpal tarsus is substantially less inflated distally and the terminal "brush" has fewer setae. The tergal prominences are either absent or very small in comparison to the adult, and the tubercles associated with the sternal setae of the opisthosoma are less developed. The free terminal lobe of the genital operculum is absent, and the coxapophyses of leg 1 are clearly visible.

DISCUSSION

There are several potential problems in the taxonomy of *Austropsopilio* that will require a generic revision to resolve, although such an undertaking will be hindered by the small number and limited accessibility of specimens. First, the genus was originally described from an immature individual (Forster 1955) and, given the substantial differences in morphology of immatures and adults in *A. sudamericanus*, it is possible that the generic diagnosis is not strictly applicable even to adults of the type species. For example, early instars of *A. sudamericanus* have tergal spines but lack the large spine-bearing prominences of the adult. Indeed, it is possible that either *A.*

altus or *A. cygneus* is synonymous with the generic type species, *A. noveahollandiae*. Second, Shear (1975, 1996) has argued that *Tasmanopilio* is similar enough to *Austropsopilio* to warrant synonymizing the genera. Indeed, the absence of an elongate eye tubercle in *Tasmanopilio* was the principal criterion cited by Hickman (1957) for distinguishing this genus from *Austropsopilio*, and this distinction has been eliminated with the discovery of *A. sudamericanus*. Furthermore, the pedipalps of the two genera are very similar (Shear 1996). Specifically, most articles of the pedipalp (i.e., trochanter to tibia) have at least one large spine-bearing apophysis and the tarsus of the female is expanded distally, has a brush-like array of setae, and lacks a claw. In addition, the two genera have a single spine-bearing tubercle on the proximal superior surfaces of the pedal basitarsi (Forster 1955; Hickman 1957; Cantrell 1980; Figs. 9, 10). Still, while it is clear that *Tasmanopilio* and *Austropsopilio* are very similar, it may be possible to offer a modified generic diagnosis for *Austropsopilio* that excludes *Tasmanopilio*: (1) a single anterior pair of protuberances on the eye tubercle; (2) spine-bearing tubercles on the carapacal margin; and (3) opisthosomal tergum with spine-bearing tubercles or prominences. It remains for a taxonomic revision, preferably informed by acquisition of new material and phylogenetic analysis, to determine whether *Austropsopilio* and *Tasmanopilio* should be synonomized.

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SPATIAL STRATIFICATION IN LITTER DEPTH BY FOREST-FLOOR SPIDERS

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ABSTRACT. Two novel sampling techniques were used to survey the spider community of the leaf litter in a deciduous forest in Kentucky, USA. Using modified pitfall traps and litter-grab techniques, we sampled separately the top, middle and bottom litter layers from April–October. Our sampling program captured over 3,000 spiders encompassing 18 different families. Both techniques revealed that the web-spinning families were more abundant in the lower litter layers. In contrast, the non-web building cursorial spiders, which actively pursue their prey, were more abundant in the top litter layer. Cursorial spiders, on average, were larger than the web-building spiders found in the leaf litter. Web-building spiders from the top litter layer were also larger than the web-building spiders caught in the middle and the bottom litter layers.

Comparison between the two sampling techniques revealed that the spider community profile is greatly influenced by the sampling method employed. The stratified litter-grab technique revealed the numerical dominance of Dictynidae (38% of the spiders captured) and Linyphiidae (32%), families that are predominately minute web-building spiders. In contrast, the pitfall-trap technique suggested Lycosidae (24%), a family of active foragers, to be numerically dominant, with Dictynidae representing only 1% of the spiders captured. The results indicate that major groups of spiders differ in their vertical distribution within deciduous leaf litter, and that sampling method can dramatically affect inferences about spider community structure.

Keywords: Micro-habitat segregation, leaf litter, pitfall trap, spider community

Spider communities that inhabit the leaf litter of an eastern deciduous forest floor frequently exhibit both high family diversity (>15 families) and numerical abundance (Kaston 1972; Dindal 1990; literature reviewed in Wise 1993). This pattern of high abundance and diversity is intriguing, considering that spiders are size-dependent generalist predators that often exhibit both intraguild predation and cannibalism (Polis 1988; Wise 1993; Wagner & Wise 1996, 1997). Research has suggested that the structural complexity of the leaf litter itself may facilitate the persistence of this high diversity of predators. In a series of field surveys and innovative field manipulation studies in mature deciduous forests in the eastern USA, Uetz (1975, 1977; 1979a, 1979b) and others (Bultman & Uetz 1982, 1984; Stevenson & Dindal 1982) examined the effects of litter complexity (e.g., leaf shape, litter depth), litter nutritional quality, prey abundance, and abiotic factors (e.g., moisture) on spider community diversity. Although prey abundance accounted for a statistically significant amount of variation in spider family diversity during the early summer months, litter depth, complexity and temperature were more important during mid- and late season (Uetz 1975, 1976, 1979a). One possible explanation may be that as the structural complexity of the litter increased, the surface area and diversity of potential foraging spaces within the leaves also increased. In particular, the spaces within curled leaves, the underside of twisted leaves, or the gaps between leaves create unique foraging sites for a diversity of spiders (Stevenson & Dindal 1982; Uetz 1991).

In addition to litter structural complexity contributing to spider family diversity, variety in spider foraging techniques may also allow for species coexistence. Spiders exhibit two basic forms of foraging techniques; entrapment, i.e. web-building spiders, or direct capture without the aid of a web, i.e. cursorial spiders (Wise 1993; Foelix 1996). These two forms of hunting techniques represent the ends of a continuum with numerous variations in between (Uetz 1992). Variation in foraging techniques may allow spiders to exploit different microhabitats within the leaf litter.

We propose that changes in structural and spatial complexity within the litter layer correlate with spider foraging methods to promote spider family diversity. In particular, spiders can exhibit habitat partitioning by restricting their foraging to particular litter layers. The layering within the litter often correlates with the age, and thus the degree of degradation, of different year-classes of litter: upper litter is composed of new, complete leaves with large air spaces between them, whereas the bottom litter layer consists of compacted humus. As a result we also expect spider species to segregate by size, with large animals in the upper, and smaller animals in the lower litter layers. The change in physical space within the different litter layers could also influence whether active pursuit or entrapment foraging method is favored. Based on these predictions we designed a field study to determine if forest-floor spiders exhibit spatial partitioning within the leaf litter in a deciduous forest. We devised two new types of sampling protocols, modified pitfall traps and stratified litter-grabs, to selectively sample the top, middle, and bottom litter layers in order to determine if spiders were non-randomly distributed within the litter according to their size and foraging mode.

METHODS

The research was conducted in an oak-hickory-maple forest in Madison County, Kentucky, USA. We devised two new sampling methods (stratified pitfall trapping and stratified litter-grab with extraction) to collect spiders at three different depths within the litter. The three litter layers corresponded to their age. The top layer was defined by the presence of curled, open-spaced leaves of the previous year. The thickness of the top litter layer fluctuates during the season. The middle layer (1–2 cm) sampled was formed by compressed leaves from several years in various degrees of decomposition, but still with a recognizable structure. The bottom stratum (1–2 cm) was identified as the amorphous humus layer that was delimitated below by a sharp boundary of clay.

Stratified pitfall traps.—Each trap consisted of a 20 cm piece of ~ 7.5 cm diameter PVC pipe sleeve which housed a cup of 50: 50 glycol:water solution with detergent added to reduce surface tension. A 1.2 cm slit was cut into the PVC sleeve either 5 cm from the end for the top or bottom-litter traps, or in the middle of the sleeve for the middle-layer trap. Two thin strips of metal flashing were attached at the top and bottom of the slit opening and extended 2.5 cm out from the pipe (Fig. 1). These lip barriers were designed to capture selectively only those spiders that moved laterally at the specific litter depth, by reducing accidental capture of animals making vertical migrations along the pipe sleeve. In the first month of sampling (April 1995), 30 pitfall traps were placed 3–6 m apart in repeating sequential order (bottom, middle, and top litter-layer sampled; $n = 10$ for each type of trap) along a circular transect 50 m in diameter. We recognized that this sequential protocol could create spatial correlation in the data; therefore, the pitfall traps were rearranged in random order for the remainder of the season (May–September 1995). The traps were emptied every two weeks.

Although pitfall trapping is an effective technique for sampling some spiders (Uetz & Unzicker 1976), the rate of capture is influenced by both abundance and activity levels of the target organism (Southwood 1978). Thus, less active spiders, e.g., many of the web-building guild, or very active and nimble spiders with excellent sense of sight, e.g., salticids (Land 1985) can be under represented in pitfall trap samples. To address this bias, a stratified litter-grab technique was developed that captured spiders that colonized layers of nylon mesh net placed at the top, middle, or bottom litter layers.

Stratified litter-grab technique.—Within the area circumscribed by the pitfall traps, two perpendicular 50 m transects were created to determine the random sampling areas to place stratified nets. Stratified litter-grabs were col-

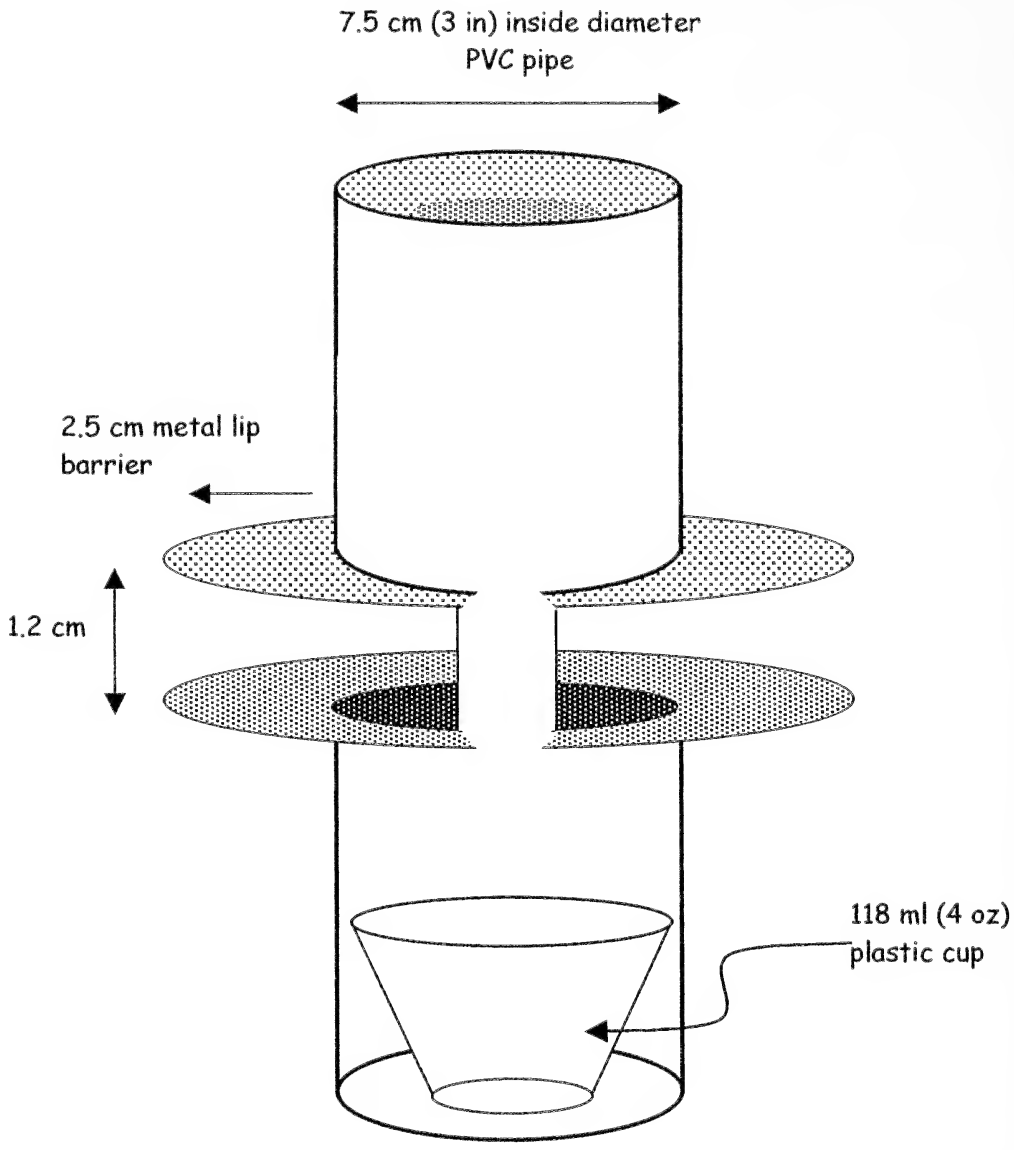

Figure 1.—Pitfall trap designed to selectively trap spiders moving laterally at a specific litter depth. The slit opening was set to one of three specific heights: the bottom, middle or top litter layer. The bottom layer sampled was the humus layer just above the soil. The middle layer was the compact litter layer between the humus layer and the top of the leaf litter. To sample the top layer, the lower lip barrier rested on top of the litter.

lected three times during the trapping period (May, July and October 1995) with each sample effort consisting of 10 litter-grab samples. Each litter-grab sample was created by first placing 0.5 m × 0.5 m pieces of mesh (3 mm) netting between the top and middle, and between the middle and bottom, litter layers (Fig. 2). To install the nets, first a sharp knife was used to cut through the litter around the area of the netting. Then the top and middle litter layers were carefully placed on separate pieces of netting. These two layers were then returned to their original position by stacking them, in order, on top of the undisturbed humus layer. The netting that separated the three layers was then secured in place by thin metal pins placed in each corner. After 4–5 weeks, a time period that allowed colonization by spi-

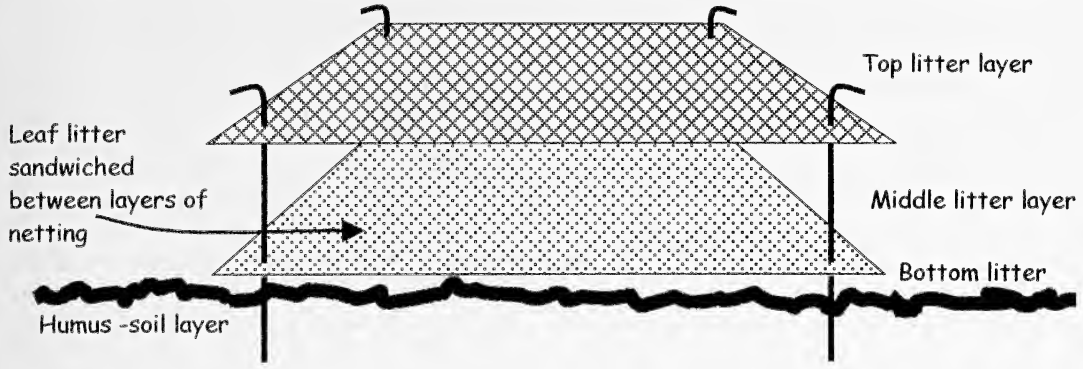

Figure 2.—The stratified litter grab technique employed two layers of netting that separated the top, middle and bottom litter layers.

ders, the anchor pins were gently removed from the four corners and the top and middle litter layers were quickly lifted and placed in separate plastic bags. The bottom humus layer was then collected by hand and placed in a third bag. All layers were first sorted by hand to remove the large spiders and were then extracted with a Tullgren funnel (Southwood 1978) to remove the smaller animals. Spiders were preserved in 70% EtOH, measured for total length (mm), and identified to family. Because we sought to uncover broad patterns, spider community structure was defined in terms of relative abundance of the major spider families. All spider families were assigned a foraging mode, either cursorial or web-building, based on published descriptions (Comstock 1940; Kaston 1972, 1981).

Statistical analysis.—Numbers of spiders in the samples often deviated substantially from a normal distribution; therefore, the non-parametric Kruskal-Wallis ANOVA (Siegel 1956) was used to determine if spider foraging modes were nonrandomly distributed across litter layers. If the Kruskal-Wallis test revealed a significant effect of litter depth, separate Mann-Whitney U tests (Siegel 1956) were conducted to test for differences between specific litter layers. Because we changed the trapping protocol for the pitfall traps after the first month of sampling, the pitfall data were analyzed as two different data sets: April, and the remainder of the months pooled for each trap. Each data set consisted of 10 independent estimates of numbers of spiders at each litter depth. In the analysis of the stratified litter-grab data, each sampling period (May, July, October) provided an independent estimate of spider distribution, since new nets were installed each month. Thus, for the Kruskal-Wallis ANOVA of the litter-grab samples there were 30 (10 nets × 3 sampling dates) independent estimates of numbers of spiders in each litter layer.

A cluster analysis (StatSoft 1995) was conducted to evaluate the similarity in composition of the spider communities, at the family level, for each depth within the leaf litter. Cluster analysis was also used to examine how similar the various spider families were in their distribution by litter depth, and how similar they were in frequency of capture by trapping technique. The cluster analysis was conducted on total counts of spiders in each family captured at each depth by each trapping method. The complete linkage (farthest neighbor) amalgamation method was employed to create the clusters. This method separates clusters based upon the greatest distance between any two objects in the different clusters (StatSoft 1995).

Spider size data was analyzed only from the stratified net samples. A Spearman Rank Order correlation was calculated between spider size, guild and litter depth (Sokal and Rohlf 1995).

RESULTS

Spider community.—The combined sampling effort yielded 3,204 spiders; 23% (747) were captured in pitfall traps and 77% (2457) were obtained from stratified litter-grab samples (Table 1). Five of the 18 spider families (Antrodiaetidae, Atypidae, Anyphaenidae,

Hahniidae, and Theridiidae) were represented by fewer than 10 individuals, and were excluded from the statistical analysis because of their rarity.

Spider foraging mode and litter depth.—Spiders numbers were not distributed uniformly across the litter layers; furthermore, the pattern of distribution with litter depth was different for the two spider foraging modes. In the April pitfall data, cursorial spiders were found significantly more often in the upper litter layers [$H_{(2,30)}$ (non-parametric Kruskal-Wallis ANOVA) = 16.5; $P < .001$), whereas web-building spiders were evenly distributed by litter depth ($H_{(2,30)} = 1.5$; $P = .48$) (Fig. 3A & B). The pitfall trap data for the remainder of the summer exhibited a similar pattern. Cursorial spider abundance varied significantly with litter depth ($H_{(2,30)} = 20.3$; $P < .0001$), with most of the cursorial spiders in the top litter layer (Fig. 3C). Although web-building spiders exhibited a trend towards having a greater abundance in the lower litter layer (Fig. 3D), the trend was not statistically significant ($H_{(2,30)} = 5.76$; $P = 0.056$). The stratified litter-grab technique revealed a clear relationship between spider abundance and litter depth. Similar to the pitfall trap data, cursorial spider abundance was significantly influenced by litter depth ($H_{(2,90)} = 53.58$; $P < .0001$), with more spiders in the top litter layer (Fig. 3E). Web-building spider abundance also exhibited a significant relationship with litter depth ($H_{(2,90)} = 39.93$; $P < .0001$), but the pattern was the opposite, with more web-building spiders found in the lower litter layers than the top layer (Fig. 3F).

Cursorial and web-building spiders displayed different distribution patterns, but within each foraging mode the two sampling methods revealed similar patterns of distribution across litter depth. However, the two sampling techniques yielded strikingly different estimates of the relative abundance of spider families within the same foraging mode (Table 1). Lycosid spiders were the most frequently captured cursorial spiders in the pitfall traps. In contrast, clubionids and gnaphosids were the most abundant cursorial spiders in the stratified litter-grab samples. For the web-building spiders, Agelenidae was the most abundant family captured in the pitfall traps, whereas Dictynidae was the most abundant web-building family in the stratified net samples.

Spider community composition by litter depth.—Cluster analysis revealed that the composition of the spider community differed with litter depth and sampling protocol (Fig. 4). The spider community captured in the bottom and middle litter layers of the net samples differed distinctly from the spider communities represented in the top litter-layer samples from the net traps, and from the pitfall traps at all depths. The spider community from the bottom and the middle litter layers of the pitfall traps also differed distinctly from those represented in the top litter layers from both nets and pitfall traps.

Cluster analysis of spider families.—Cluster analysis of the spider families based upon trap type and litter depth revealed distinct groupings (Fig. 5). This analysis indicates which spider families are most similar based upon the depth of the litter they inhabit and the type of trap used to capture them. The first distinction was between two web-building families, Dictynidae and Linyphiidae, and all other spider families. The second major grouping segregated agelenids and lycosids from two other clusters that were composed of common cursorial spider families (Clubionidae, Gnaphosidae and Thomisidae) and an amalgamation of cursorial and web-building spiders (Amauboridae, Segestridae, Salticidae, Araneidae, Ctenidae and Nesticidae).

Spider size and litter depth.—Spider size differed with litter depth ($r_s = 0.259$; $P < 0.001$) and foraging mode ($r_s = -0.702$; $P < 0.001$) (Fig. 6). At all litter depths, cursorial spiders were significantly larger than web-spinning spiders. Among the web-spinning spiders, individuals from the top litter layer were larger than those caught in the middle and the bottom layers (Fig 6).

DISCUSSION

In a manner analogous to fish and plankton exhibiting species-specific vertical stratification in the water column (e.g., Holliday and Larsen 1979, Roepke 1993, Gray 1998), spiders exhibit taxon-specific (family level) vertical stratification within the depths of the forest-floor leaf litter. Our use of two separate and novel sampling methods, the stratified litter-grab and pitfall traps, indicated clear vertical stratification.

Table 1.—Mean and standard error for each Family captured at each litter depth (Bottom; Middle; Top layer) and trap type (Pitfall or Stratified Net). Mean represents average captured by trapping effort, e.g., number of spiders captured per pitfall trap per two-week sampling period or number of spiders captured per stratified net per month. Families identified with the "W" are web-building spiders; those labeled with a "C" are cursorial spiders. Families not identified by foraging guild were excluded from other analysis because of low capture rates. Numbers in bold represent the family with the highest average capture rate for that litter layer and trap type.

		Leaf litter depth					
		Bottom layer		Middle layer		Top layer	
		Pitfall	Nets	Pitfall	Nets	Pitfall	Nets
W	Agelenidae	**0.60 ± 0.10**	2.0 ± 0.35	0.43 ± 0.07	2.24 ± 0.30	0.51 ± 0.10	0.53 ± 0.34
W	Amaurobiidae	0	0	0.06 ± 0.03	0.14 ± 0.08	0.09 ± 0.04	1.40 ± 0.35
W	Araneidae	0.01 ± 0.01	0.81 ± 0.56	0	0.17 ± 0.17	0.03 ± 0.02	0
W	Dictynidae	0.01 ± 0.01	**16.11 ± 3.73**	0.03 ± 0.02	**16.28 ± 2.41**	0.03 ± 0.02	1.07 ± 0.33
W	Linyphiidae	0.46 ± 0.10	11.81 ± 2.45	0.42 ± 0.09	13.83 ± 2.49	0.17 ± 0.06	2.87 ± 0.42
W	Nesticidae	0.22 ± 0.05	0	0.07 ± 0.03	0	0.02 ± 0.02	0
W	Segestriidae	0.01 ± 0.01	0	0.02 ± 0.02	0.10 ± 0.06	0.02 ± 0.02	1.20 ± 0.47
C	Clubionidae	0.14 ± 0.05	0.26 ± 0.09	0.20 ± 0.05	1.83 ± 0.39	0.22 ± 0.04	**5.13 ± 0.90**
C	Ctenidae	0.10 ± 0.04	0	0.06 ± 0.03	0.03 ± 0.03	0.09 ± 0.03	0.33 ± 0.19
C	Gnaphosidae	0.09 ± 0.03	0.19 ± 0.08	0.29 ± 0.07	1.34 ± 0.32	0.64 ± 0.11	4.20 ± 0.96
C	Lycosidae	0.17 ± 0.05	0.19 ± 0.08	**0.56 ± 0.11**	0.38 ± 0.13	**1.28 ± 0.27**	1.93 ± 0.67
C	Salticidae	0.03 ± 0.02	0	0.03 ± 0.02	0.24 ± 0.09	0.24 ± 0.06	1.0 ± 0.20
C	Thomisidae	0.08 ± 0.03	0.11 ± 0.06	0.19 ± 0.05	1.55 ± 0.46	0.59 ± 0.13	4.53 ± 0.72
	Antrodiaetidae	0.02 ± 0.02	0	0.01 ± 0.01	0	0.01 ± 0.01	0
	Anyphaenidae	0.01 ± 0.01	0	0	0	0	0
	Atypidae	0	0	0	0.03 ± 0.03	0.01 ± 0.01	0
	Hahniidae	0	0	0.01 ± 0.01	0	0	0.07 ± 0.07
	Theridiidae	0	0.11 ± 0.06	0	0.10 ± 0.06	0	0.13 ± 0.09

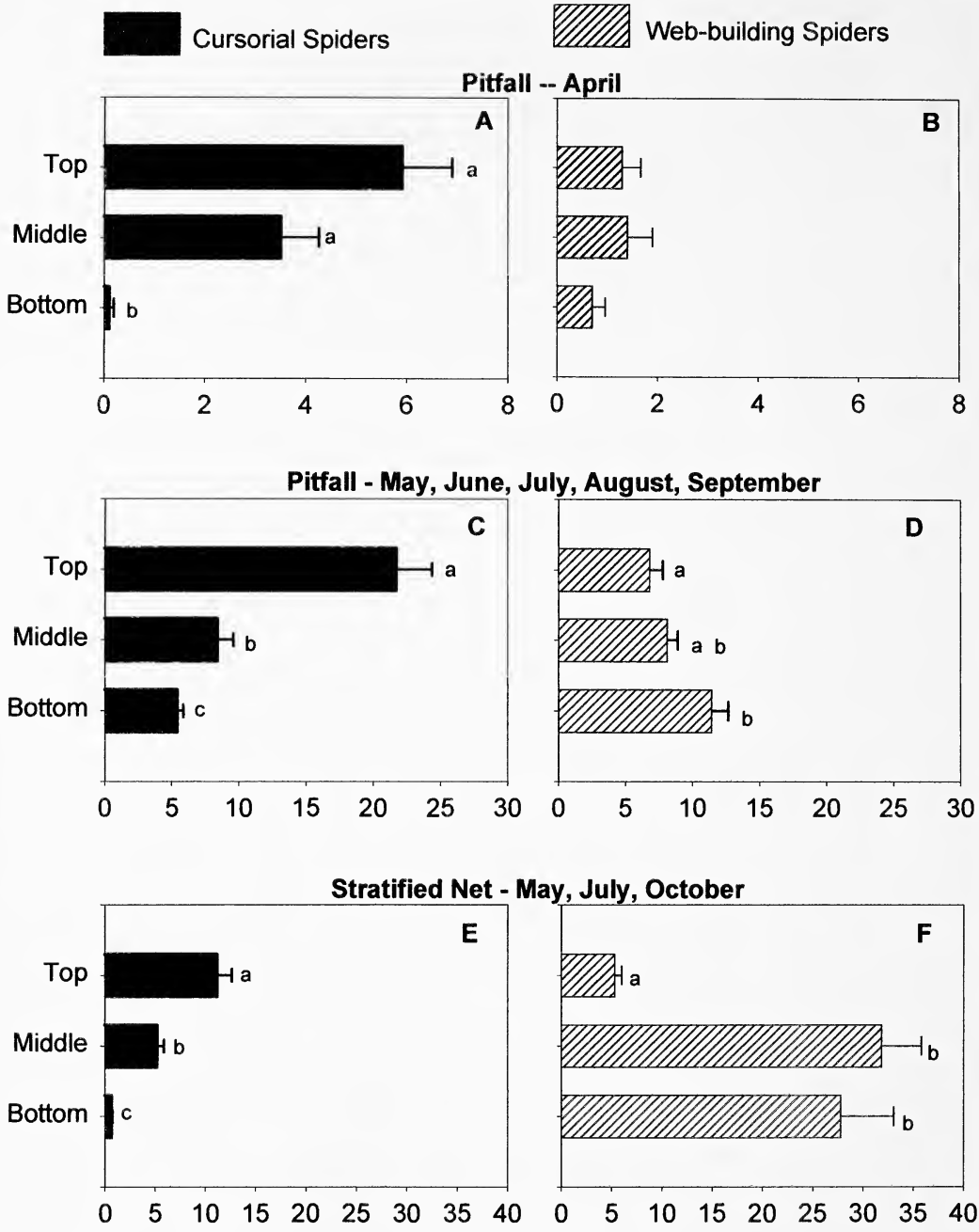

Figure 3.—Mean number (± SE) of spiders captured at each litter depth by both sampling methods (stratified litter grab [net] and stratified pitfall sampling). Plots A & B are from the pitfall data collected in April. Plots C & D represent data from the pitfall traps for the remainder of the season. Plots E & F represent data from the stratified litter grab technique. Bars labeled with the same letter are not significantly different based upon a Mann-Whitney U test. Absence of letters indicates that the Kruskal-Wallis H statistic was not significant at the 0.05 level.

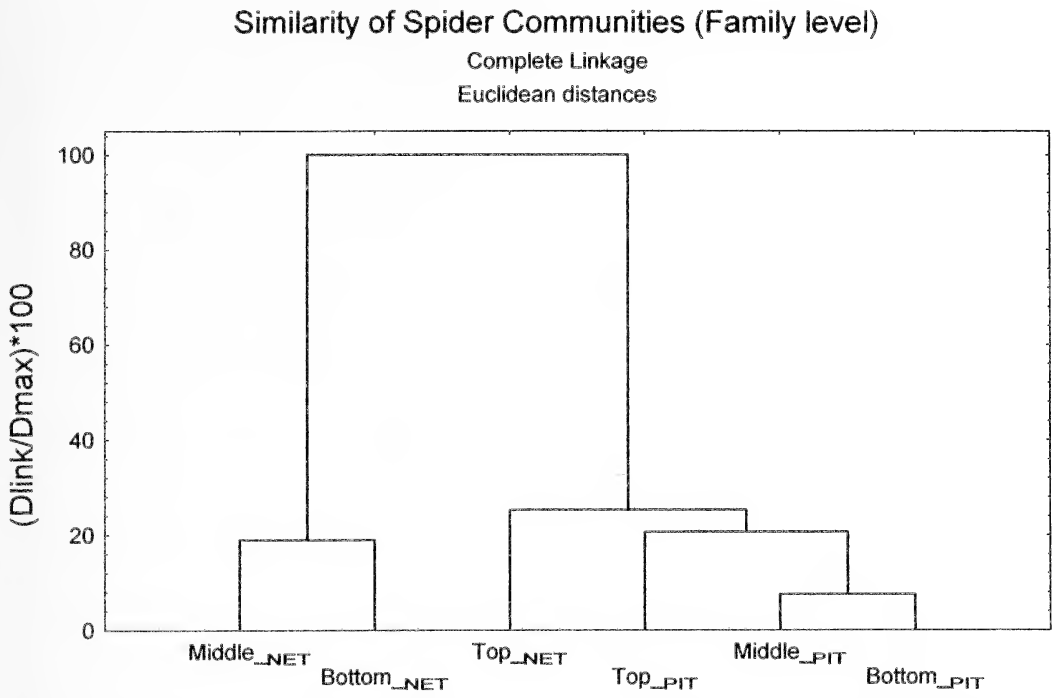

Figure 4.—Cluster analysis of spider community similarity based upon litter depth and trapping method. Spider family-level communities of the bottom and middle litter layers were distinctly different than the spider family-level communities found at the top litter layer. Spider communities were most similar between bottom and middle layers from the net data, and bottom and middle layers of the pitfall data. The composition of the spider community differed based upon sampling method.

Taxonomic groupings within the diverse spider community of the forest floor exhibit consistent microhabitat segregation correlated with litter depth. Cursorial spiders, which typically actively pursue or use a sit-and-wait strategy for prey capture (Uetz 1992), preferentially inhabited the top litter layers. In contrast, the web-building spiders were concentrated in the middle and lower litter layers. In conjunction with the shift in foraging mode with litter depth, body size of spiders decreased with litter depth. The main distinction in size was between those spiders captured in the top litter layer compared with those captured in the middle and bottom litter layers. The observed correlation in size of spiders with litter depth reflected large cursorial species occupying the upper spacious litter, while small web-building spiders occupied the older, compacted litter in the lower layers. On average, cursorial spiders were larger than web-spinning spiders, even when controlling for effects of litter depth. The low abundance of cursorial spiders in the bottom layer may be related to their inability to penetrate the compacted, lower litter layers. However, space limitation does not explain the absence of the smaller web-building spiders from the top litter layers.

Various factors may be contributing to the difference in the size and type of spiders found with litter depth. Abiotic factors, such as moisture, light, and temperature, may influence spider distribution if they differ dramatically between the top and bottom of the litter layer. In the thick litter layer of a deciduous forest, relative humidity is higher in the lower layers compared to the surrounding air (Clary & Folliot 1969; Edwards & Sollins 1973; Swift et al. 1979). Unlike some insects, spiders lack the ability to extract moisture from water vapor in the atmosphere (Pultz 1987) and many are very sensitive to desiccation. Some spiders have evolved the tarsal organ, a specialized receptor on the leg used to detect changes in humidity (Foelix 1996). Web-building spiders such as Dictynidae, Amaurobiidae, and

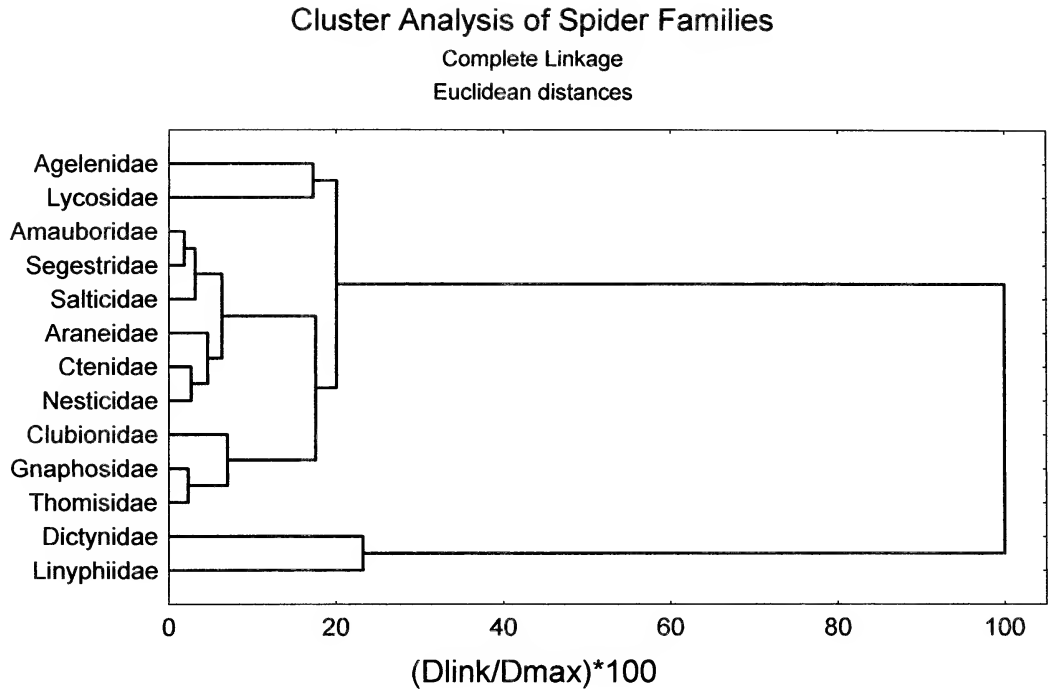

Figure 5.—Cluster analysis of spider families based upon litter depth and sampling method. Spider families closely grouped were similar in their use of litter depth and susceptibility to trapping methods.

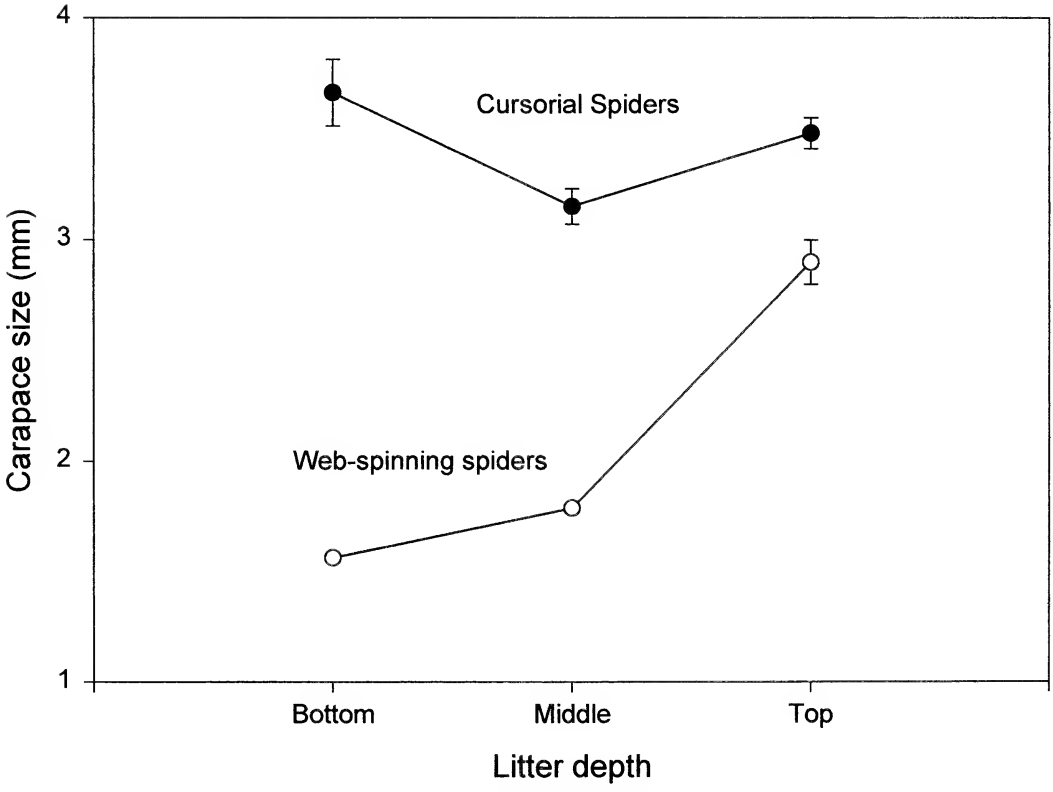

Figure 6.—Mean spider size (± SE) by foraging method and litter depth.

Linyphiidae may be restricted to the lower litter layers since these smaller spiders have a large ratio of surface area to volume, which could make hygrothermal regulation more difficult in the upper litter layers. In support of this interpretation, not all the web-building spiders were restricted to the lower layers. Based on the pitfall trap data, the large funnel-web agelenids were equally distributed across litter depths. The funnel-web design of some agelenid spiders allows them to live in a retreat that is deeper in the litter layer, thereby protecting them from desiccation (Riechert 1976). In contrast, the larger, more active cursorial spiders may be able to reside in the upper litter layer since they can more readily relocate to shady or moist locations when temperature and moisture levels are unacceptable (Humphreys 1987).

Ambient light intensity is another abiotic factor that may influence spider distribution within the leaf litter. Decreased light availability in the lower litter layers may hinder prey capture by visually oriented cursorial spiders. Although some cursorial spiders rely on vibratory cues to locate prey, reliance on visual cues for prey detection is important for lycosids and salticids (Land 1985; discussed in Foelix 1996). The lycosid *Schizocosa ocreata*, a species of the dominant wolf spider genus collected in this study, is known to rely on visual detection of prey when determining a foraging site (Persons & Uetz 1996), which may limit them to the upper litter layers. The importance of vision in prey capture in other cursorial spiders, e.g., Clubionidae and Gnaphosidae, is poorly understood. Web-building spiders typically have poorly developed eyes (Foelix 1996) and may be less hindered in capturing prey in the darker, lower litter layers.

Our sampling program captured over 3,000 spiders encompassing 18 different spider families. Comparison between sampling efforts, pitfall traps versus litter-grab sampling, indicates that the inferred spider community profile is greatly influenced by the sampling method employed. Studies that rely on pitfall sampling to characterize the leaf-litter spider community inherently over-emphasize the abundance of cursorial spiders in comparison to web-building species. In our pitfall traps, cursorial spiders made up 60% of the total spiders captured; in comparison, in the stratified litter-grab samples cursorial species accounted for only 21% of the spiders collected. The largest discrepancy was in the representation of the web-building Dictynidae and cursorial Lycosidae. Data based on pitfall traps suggest that lycosid spiders are abundant and dictynid spiders are rare. However, density estimates from the litter-grab samples indicate the opposite. Average summer density for dictynids was about 124 individuals/m^2 in contrast to the average estimated density of lycosid spiders of 7 individuals/m^2. These results clearly show how spider activity and sampling method can bias the representation of a spider community.

Our data also indicate that the composition of the spider community at the family level changes from the top to lower litter layers. In the top layers the spider families representing cursorial species were the ones numerically dominant in the samples. In the middle and lower litter layers, those spider families recognized as web-building foragers were the numerically dominant group. We suggest that the complex 3-dimensional space within the leaf-litter layer may facilitate the high spider family diversity observed in the forest floor. Other researchers have found that the physical structure of the habitat itself directly influences spider community composition (Robinson 1981; Uetz 1991; Balfour & Rypstra 1998; Halaj et al. 1998). What is not clear is the relative role played by abiotic factors versus interspecies interactions in influencing the shift in spider community composition with litter depth. Future removal studies of some of the numerically dominant cursorial and web-building spiders within this system could reveal the role of biotic interactions in creating the observed community diversity and microhabitat distribution.

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ANYPHAENA (ARANEAE, ANYPHAENIDAE) OVERWINTERING ON LOWEST LIMBS OF WHITE OAK

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ABSTRACT. Juvenile *Anyphaena* sp. were collected from overwintering traps placed on the lowest limbs of white oak, *Quercus alba*, in South Carolina. Multiple regression analysis was used to determine that the number of juvenile *Anyphaena* sp. found can be predicted by the circumference of the limb, the distance from the trunk and the distance from the ground. This study helps demonstrate that the limbs of trees, although often neglected in overwintering studies, can provide a refuge for arthropods.

Keywords: *Anyphaena*, overwintering, *Quercus alba*

Many spiders enter a dormant stage during winter conditions (Schaefer 1977) and those that overwinter on the trunks of trees are often surveyed by collecting the spiders with cardboard wrapped around tree trunks (Tamaki & Halfhill 1968; Tedders 1974; Fye 1985; Mizell & Schiffhauer 1987; Pekar 1999; Horton et al. 2001). However, the species collected in the trunk traps are not necessarily the same species that are collected during warmer months from the limbs of the same trees (Pekár 1999; Horton et al. 2001) and the limbs are usually neglected when sampling for overwintering species. Our research was conducted to determine if the limbs of white oak trees, *Quercus alba* L., were suitable for arthropods to overwinter, and, if so, where on the limbs they overwintered.

METHODS

We made traps of gray coroplast (corrugated plastic, similar to cardboard) by cutting a sheet of coroplast into sections 15 cm long by 3–3.5 cm wide, providing six longitudinal cavities in each trap. We placed traps on three mature white oak trees, *Quercus alba* L., on 30 October 1998. One tree was located in Pickens County, South Carolina on the Clemson University campus. Two trees were located in Greenville County, South Carolina, one on the Bob Jones University campus and the other at Reedy River Falls Historical Park. Trees were selected based on ease of accessibility. Three sets of traps were placed on limbs greater than or equal to 3 m in length: one trap set was proximate to the trunk, one was in the middle of the limb, and one was on the terminus of the limb. Two sets of traps were placed on limbs shorter than 3 m in length: one trap set was proximate to the trunk and one on the terminus of the limb. We placed traps around the limb 2.5 cm apart, parallel to the limb, and held them in place with gray duct tape. The diameter of the limb determined the number of traps around the limb. Two groups of traps were place around the limb 3–6 cm apart, one offsetting the other (Fig. 1).

We used 5 limbs on the oak tree in Pickens County, each with 3 sets of traps. On the tree at Reedy River Historical Park in Greenville County we used three limbs, each with 2 sets of traps, and on the tree at Bob Jones University we used two limbs, each with 3 sets of traps. We used a total of 27 traps. The number of limbs used was based on the number of limbs reachable at each location with a 3 m ladder. For purposes of regression analysis the average circumference of the limb at each trap (circumference at both ends of the trap set divided by 2), the distance of the trap from trunk, the distance from the trap to the ground, and the branching of the limb from the trunk to the trap were measured. The bark surface was rated on a scale of 1–3, where 1 = smooth and 3 = rough.

Figure 1.—One set of coroplast strip traps.

Traps were removed 24 February 1999 after three consecutive days of average daily temperatures near freezing (±1 °C) (average temperature for Greenville County was 0.9 °C for 22–24 Feb. and −0.4 °C for Pickens County). Traps were placed in plastic bags, taken to the lab and placed in the freezer. Specimens were removed from the traps, separated, preserved in 80% ethanol and identified. Voucher specimens were placed in the Clemson University Arthropod Collection.

Juvenile *Anyphaena* sp. were the only arthropods found in numbers large enough to conduct multiple regression analysis. The total number of *Anyphaena* sp. collected was 340. Multiple regression analysis was conducted using Minitab. The dependent variable was the number of *Anyphaena*, which was standardized for each trap set by dividing the total number of *Anyphaena* by the total number of traps in each set. The independent variables were average circumference of the limb, distance from the trunk, distance from the ground, number of branches per limb, and bark surface scale for each trap set.

For multiple regression analysis on *Anyphaena* no transformation of the dependent variable was needed. A tolerance test showed multicolinearity between polynomials of the independent variables and the independent variables. Therefore, only the raw independent variables were used in the analysis. Stepwise, forward, and backward model selection techniques all provided the same model. The model showed no systematic patterns, no outliers, and no evidence of lack of fit.

RESULTS

Spiders were the most numerous arthropods collected. All the arthropods collected are listed in Table 1. More *Anyphaena* sp. were collected near the trunk than the terminus of the limbs (Table 2).

The multiple regression analysis provide the following model: Number of *Anyphaena* sp. = −16.1 + 20.3 (circumference of limb) − 2.74 (distance from the trunk) + 9.86 (distance from the ground). This model, with an R^2 of 70.0%, shows that the number of *Anyphaena* overwintering in traps on the bottom limbs of *Q. alba* can be predicted by the circumference of the limb, the distance from the trunk and the distance from the ground.

DISCUSSION

Schaefer (1977) studied the overwintering habits of spiders and determined four overwintering habit types. *Anyphaena* sp. is part

Table 1.—Arthropods collected from overwintering traps around limbs of white oak.

Class	Order	Family	Species
Arachnida	Araneae	Agelenidae	*Coras* sp. juv.
		Anyphaenidae	*Anyphaena* sp. juv.
		Araneidae	*Araneus* sp. juv.
		Philodromidae	*Philodromus vulgaris* (Hentz)
			Philodromus sp. juv.
		Salticidae	*Eris militaris* (Hentz)
			Hentzia mitrata (Hentz)
			Metacyrba undata (De Geer)
		Thomisidae	*Bassaniana versicolor* (Keyserling)
Diplopoda	Polyxenida	Polyxenidae	*Polyxenus fasiculatus* (Say)
Insecta	Blattaria	Blattellidae	*Parcoblatta* sp. juv.
	Diptera	Syrphidae	*Syrphus* sp. juv.
	Hemiptera	Miridae	*Deraeocoris nebulosus* (Uhler)
	Psocoptera	Ectopsocidae	*Ectopsocus meridionalis* Ribaga

of the majority (45%) of spiders that overwinter in the juvenile stage (Schaefer 1977). Tree-dwelling spiders in the genus *Anyphaena* are nocturnal wanderers, typically living in foliage from spring through fall, but little of their ecology or behavior is known (Platnick 1974). They feed on aphids and other prey not typically active during the day (Marc & Canard 1997; Marc et al. 1999). *Anyphaena* spp. take refuge during the winter but can be active during warmer days (Turnbull 1960), increasing their ability for survival (Gunnarsson 1985). Other overwintering studies, that included *Anyphaena* spp., sampled only the trunk or the proximal end of the largest branch. Bajwa and AliNiazee (2001) found only four *Anyphaena* in a four year study. Horton et al. (2001) found only seven *Anyphaena* in a one year study. We demonstrated that *Anyphaena* will overwinter on most parts of the branches with refugia present.

Most refuges available to overwintering spiders are eliminated when leaves are shed. Previous studies have shown or suggested that after leaf-fall spiders move down from the crown until they find refuge (Duffey 1969; Horton et al. 2001), which might be the case with our spiders. The overwintering traps provided a refuge that otherwise would not have been available. The diameter of the limbs affected the number of spiders and without exception, the larger the diameter of the branch the rougher the bark, which might also provide refugia.

Table 2.—Mean number of *Anyphaena* sp. juv. (± SE) collected from coroplast traps on white oak, *Quercus alba* limbs (South Carolina, 1999). Limb position is relative to the trunk.

Limb position	Average # *Anyphaena* (*n*)
Proximate	17.4 ± 2.0 (10)
Middle	12.3 ± 2.8 (10)
Terminus	5.4 ± 1.3 (8)

Horton et al. (2001) collected arthropods from cardboard bands weekly 23 Aug–07 Dec 1999 in Washington apple and pear orchards. They found *Anyphaena pacifica* Banks in higher numbers (224 total) on a weekly basis than in overwintering samples (7 total, collected in Jan 2000). They suggested that the spiders overwinter elsewhere. In Oregon, *A. pacifica* was found in low numbers (0.35% of total catch) during the growing season by beating the branches over a net (Bajwa & AliNiazee 2001). In Europe, Marc et al. (1999) and Marc and Canard (1997) suggested that *A. accentuata* (Walckenaer) overwinters on the tree trunk, but they collected very few individuals (1% of total catch).

Our study provides information that can be used in further studies of overwintering arthropods on trees. The branches represent a large portion of the tree and are often neglected as a sampling site during the winter months. Large numbers of spiders on the limbs could alter decision made in integrated pest management for landscapes and orchards such as apple, peach, pear, and pecan.

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AN ANALYSIS OF THE SECONDARY STRUCTURE OF THE MITOCHONDRIAL LARGE SUBUNIT rRNA GENE (16S) IN SPIDERS AND ITS IMPLICATIONS FOR PHYLOGENETIC RECONSTRUCTION

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ABSTRACT. We investigated the pattern of molecular variation with respect to secondary structure in the 16S ribosomal RNA gene and its phylogenetic implications for arachnids with a focus on spiders. Based on a model by Gutell et al. (1996), secondary structures were proposed for the 3′ half of 16S in the mygalomorph spider *Aptostichus atomarius*. Models were also constructed for a hypervariable length of the 16S in three other arachnids, which revealed a trend of stem and loop reduction in more advanced arachnids. Using a simple statistical approach to compare functional regions, we found that internal and external loops are more variable than stems or connection regions. Down-weighting or excluding regions which code for the more variable loops improved tree topologies by restoring the monophyly of the genus *Aptostichus*, a group supported by combined 16S, COI, and morphological data in other analyses. This study demonstrated the utility of considering secondary structure for DNA sequence alignment and phylogenetic reconstruction in spiders.

Keywords: Secondary structure, 16S rRNA gene, *Aptostichus*, phylogenetic utility

The most important aspect of any molecular phylogenetic study is, unequivocally, gene choice. Choosing a gene that strikes the appropriate balance between molecular conservation and variability is essential to the success of phylogenetic reconstruction. Without question the functional role of a gene and its rate of evolution are tightly coupled although within genes, this relationship is variable because regions of a single gene can evolve at different rates. This tight relationship between rate of nucleotide substitution and gene component "form and function" results in a single gene being useful at different, sometimes quite disparate phylogenetic levels. Such multilevel phylogenetic utility, strongly tied to gene function (i.e., the functional secondary structure) is particularly true for the mitochondrial 16S rRNA gene in arthropods (Flook & Rowell 1995), the gene of focus for this paper.

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The 16S rRNA gene, which encodes the mitochondrial large ribosomal subunit (mt LSU) in animals, has been employed extensively to explore phylogenetic relationships in arthropods at most phylogenetic levels [e.g., ordinal (e.g., Flook & Rowell 1995), familial level (e.g., Black & Piesman 1994) and the genus level and below (e.g., DeSalle et al. 1992; Bond et al. 2001)]. The wide range in utility of 16S at various taxonomic levels suggests that the differential rates of molecular evolution within 16S, due to varying functional constraints, greatly affect its phylogenetic utility. Thus, understanding the functional roles of different portions of the gene through secondary structure modeling should lead to a more robust use of 16S in phylogenetic studies.

The main focus of this paper is the secondary structure of 16S in spiders and other arachnids. One of the first models of 16S secondary structure in arthropods was created by Clary & Wolstenholme (1985) using the *Drosophila yakuba* sequence. Subsequent models by Gutell and colleagues (Gutell & Fox 1988;

Table 1.—Spider taxa sampled.

Higher level classification	Species	Origin	Reference/GenBank accession #
Mesothelae			
Liphistiidae	*Heptathela nishihirai* Haupt 1979	Japan	Huber et al. 1993
Opisthothelae			
Araneomorphae			
Clubionidae	*Clubiona pallidula* (Clerck 1757)	Austria	Huber et al. 1993
Ctenidae	*Cupiennius coccineus* F. Pickard-Cambridge 1901	Costa Rica	Huber et al. 1993
Ctenidae	*Cupiennius getazi* Simon 1891	Costa Rica	Huber et al. 1993
Ctenidae	*Cupiennius salei* (Keyserling 1877)	Mexico	Huber et al. 1993
Ctenidae	*Phoneutria boliviensis* (F.O. Pickard-Cambridge 1897)	Costa Rica	Huber et al. 1993
Lycosidae	*Pardosa agrestis* (Westring 1861)	Austria	Huber et al. 1993
Pisauridae	*Dolomedes fimbriatus* (Clerck 1757)	Austria	Huber et al. 1993
Pisauridae	*Pisaura mirabilis* (Clerck 1757)	Austria	Huber et al. 1993
Mygalomorphae			
Antrodiaetidae	*Antrodiaetus unicolor* (Hentz 1841)	Virginia	AY241258
Cyrtaucheniidae	*Aptostichus atomarius* Simon 1891	California	AY241254
Cyrtaucheniidae	*Aptostichus simus* Chamberlin 1917 (3 populations sampled, Bond et al. 2001)	California	AF307969, AF307964, AF307960
Cyrtaucheniidae	*Aptostichus* sp.	California	AY241255
Cyrtaucheniidae	*Entychides arizonicus* Gertsch & Wallace 1936	Arizona	AY241257
Cyrtaucheniidae	*Promyrmekiaphila gertschi* Schenkel 1950	California	AY241256

Gutell et al. 1993) were based on extensive surveys of sequences as well as studies of positional covariance; these are thus considered to be more accurate and have been used in recent studies modeling secondary structure in arthropods (e.g. Buckley et al. 2000). Existing secondary structure models of 16S in arachnids are limited to a tick (Black & Piesman 1994), which used the Clary & Wolstenholme (1985) model and two spider species of the infraorder Araneomorphae (Huber et al. 1993; Masta 2000), which used the Gutell model (Gutell & Fox 1988). To obtain a more complete picture of arachnid 16S secondary structure, this study will examine the secondary structure of the other "primitive" infraorder of spiders, the Mygalomorphae (Coddington & Levi 1991), and, to a lesser extent, primitive liphistiid spiders, Acari (ticks) and Scorpiones using the Gutell model. Spider taxa from disparate groups were examined as part of a concerted effort to sample across all of the major clades. Table 1 summarizes the taxa used in this analysis, the classificatory placement of these taxa, and the source of their sequences. Decisions regarding taxon choice within the Mygalomorphae reflect an attempt to examine taxa across a number of phylogenetic levels within this clade.

The major objectives of this study are to: 1) construct a secondary structure model for mygalomorph spiders using the preferred Gutell model, 2) examine trends in secondary structure evolution in spiders and other arachnids, 3) analyze the pattern of molecular variation with respect to structure in mygalomorphs and araneomorphs, and 4) assess the effects that differential weighting of molecular characters based on secondary structure has on phylogeny reconstruction in spiders. This is the first study of arachnids to examine the rates of variation in 16S rRNA relative to secondary structure in a rigorous statistical manner and to analyze secondary structure trends across the class. It is also the first to consider the implications of secondary structure in se-

quence alignment and phylogenetic reconstruction in arachnids.

METHODS

DNA extractions.—Total genomic DNA was extracted from leg tissue using a Puregene DNA extraction kit, which comprises a lysis step in which ground tissue is incubated in Tris-EDTA buffer with SDS and Proteinase K for three hours, a protein precipitation step using potassium acetate, followed by DNA precipitation in isopropanol, and a 70% ethanol wash. DNA was resuspended in Tris-EDTA buffer and diluted 1:100 for subsequent reactions.

Mitochondrial gene PCR and sequencing.—The polymerase chain reaction (PCR) was used to amplify the 16S rRNA gene with the 16S universal primers 16sar-5′ (5′-CGCCTGTTTATCAAAAACAT-3′) and 16sbr-3′ (5′-CCGGTCTGAACTCAGATCACGT-3′) (Hillis et al. 1996). The primers 16sar-5′ and 16sbr-3′ correspond to *Drosophila melanogaster* mitochondrial genome positions 13398 and 12887 respectively. Standard PCR reactions were carried out in 50 µl volumes and run for 35 cycles, each consisting of a 30 sec denaturation at 95 °C, 30 sec annealing at 50°C and 45 sec (+3 sec/cycle) extension at 72°C, with an initial denaturation step of 95°C for 2.5 min and a final extension step of 72°C for 10 min. Amplification products were electrophoresed on a 0.8% agarose gel, excised from the gel and purified using Qiagen QIAquick gel extraction columns. Purified products were sequenced from both directions with an ABI PRISM 377 and 310 automated sequencers using the ABI PRISM Dye Terminator Cycle Sequencing Ready Reaction Kit with AmpliTaq DNA Polymerase, FS.

Secondary Structure.—Mygalomorph 16S sequences generated for six taxa were crudely aligned (alignment of stem regions was improved by eye once the secondary structure was obtained) with sequences from eight araneomorph taxa (Table 1) and *Drosophila melanogaster* using ClustalX (Higgins et al. 1996). The 16S rRNA secondary structure was predicted for the mygalomorph *Aptostichus atomarius* Simon 1891 (Fig. 1) by comparison with sequences and models from *Drosophila yakuba* (Gutell et al. 1993) and an araneomorph (Huber et al. 1993). We assumed that the location of stems and loops would be very similar because the LSU rRNA secondary structure has been found to be widely conserved (Buckley et al. 2000; Masta 2000). The *A. atomarius* sequence was chosen because it had the highest similarity to *Drosophila*, facilitating comparison.

To examine evolution of secondary structure in arachnids, models were also created for a hypervariable portion of the molecule (Fig. 1) in distantly related arachnid taxa: the tick *Ornithodoros moubata* (Murray 1877) (Black & Piesman 1994), the scorpion *Vaejovis carolianus* (Beauvois 1805) and the mesothele *Heptathela nishihirai* Haupt 1979 (Huber et al. 1993) (Fig. 2). All structures were drawn using Canvas© graphics software (Deneba Systems Inc.).

Analysis of variability with respect to secondary structure.—Each nucleotide position was assigned a single letter designating its structural function (S = stem, I = internal loop, L = external loop, C = connecting region) and was coded as variable (1) or invariable (0). In this study, stems refer to a series of bonded nucleotides. Internal loops are those unbonded nucleotides, which occur within a stem; external loops occur at the end of stems. Connecting regions link stems.

Variation was analyzed separately for the two spider infraorders, Mygalomorphae and Araneomorphae. For each structural category, variability was calculated by dividing the number of variable positions by the total number of positions. Statistical analyses were performed using SAS (SAS Statistical Systems).

To compare the pattern of variation across structural regions to random variation within the molecule, the percent variability of random blocks within the sequence was compared to the percent of actual variability within structural units (S, I, L, C). A simple random number generator program written for Mathematica (Wolfram 1996) produced nucleotide blocks in lengths of 5 or 13 consecutive numbers between 1 and 503 base pairs. The block size corresponds to the maximum and minimum average sizes of the structural regions, and the random numbers corresponded to positions along the molecule. The mean variability in the random blocks provided the expected values for a Chi-Squared Test to determine if the pattern of variability was distinct from the random model.

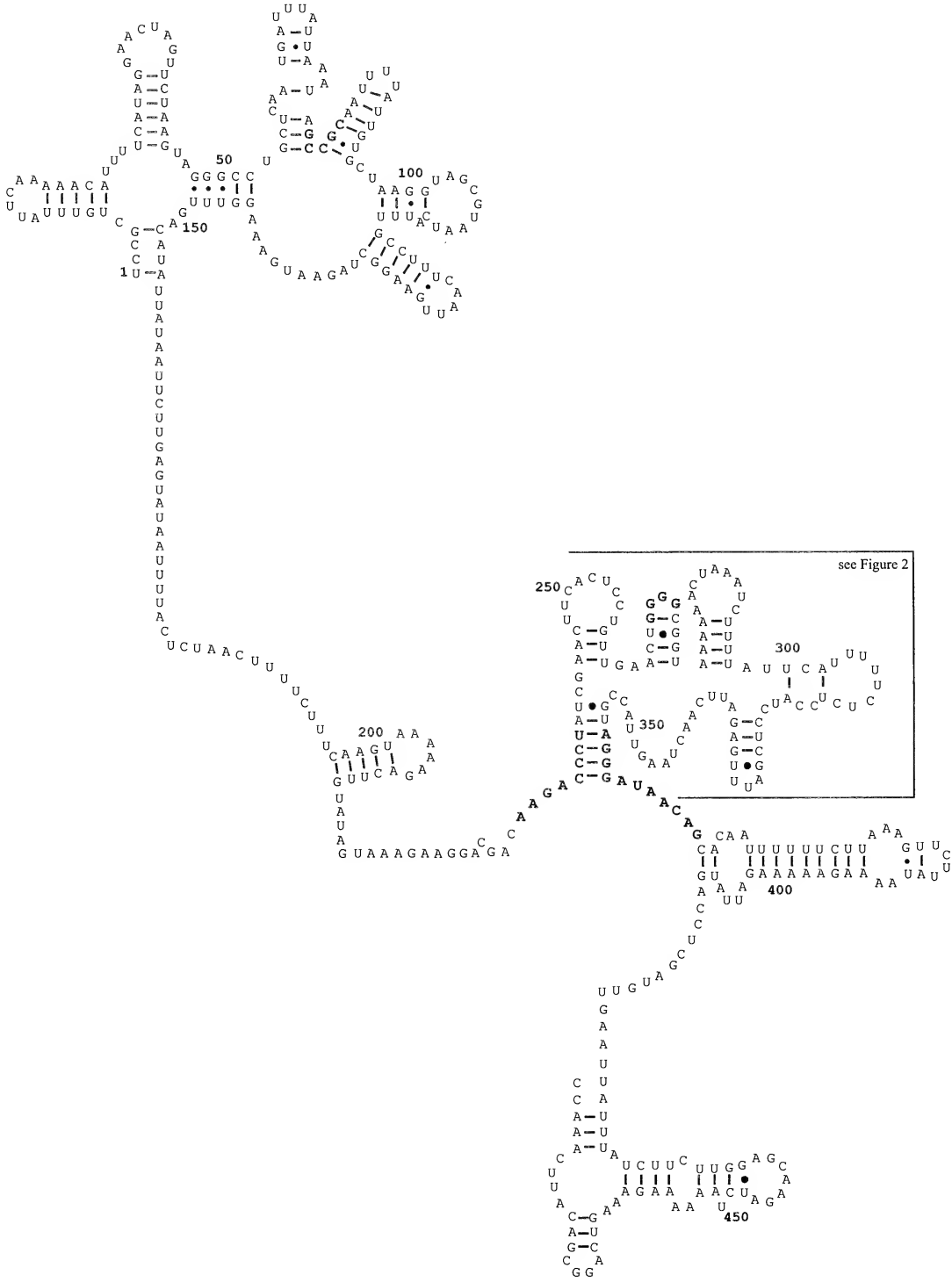
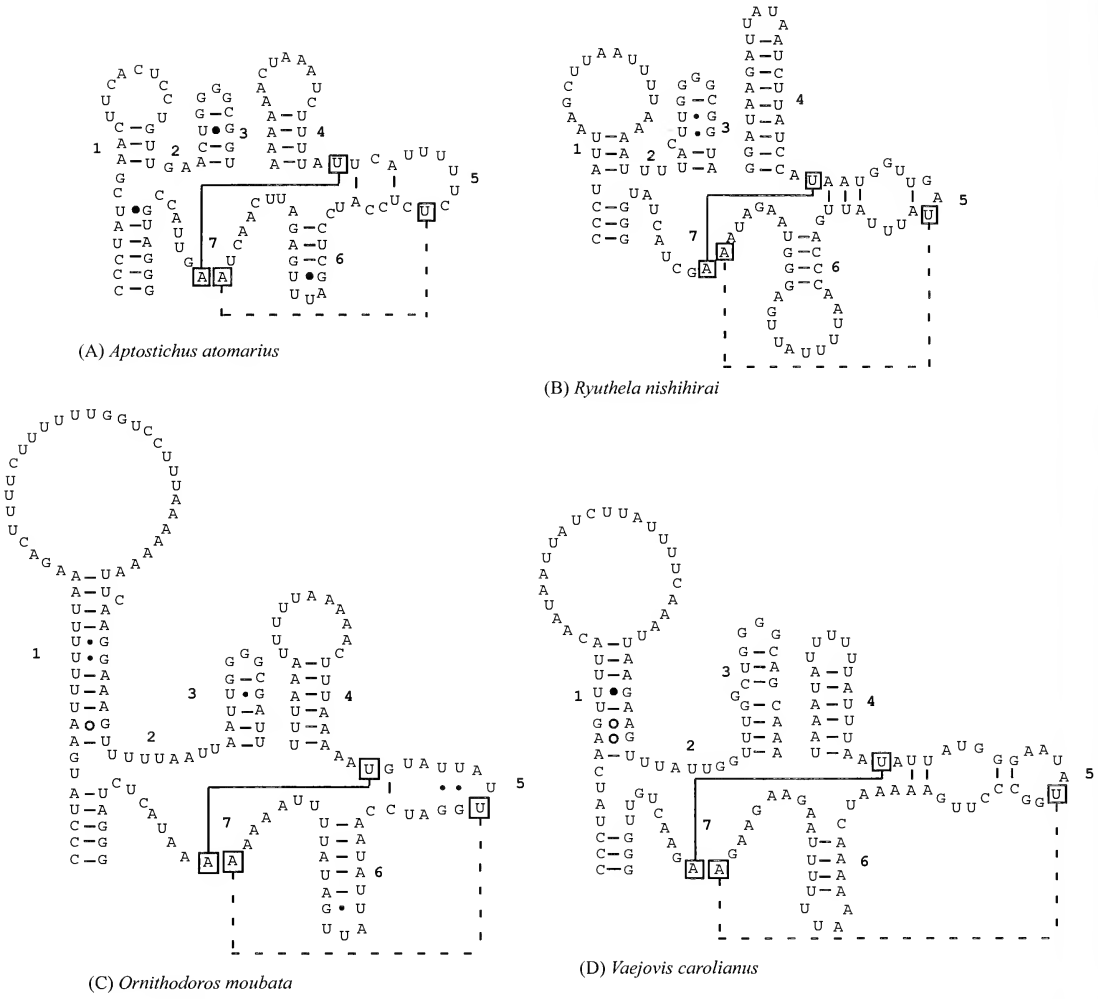


Figure 1.—Proposed secondary structure model for the 3′ half of 16S of the mygalomorph species *Aptostichus atomarius* based on the Gutell et al. model (1993). Highly conserved regions indicated by bold-lettered nucleotides. Dashes represent Watson-Crick bonds; circles are U-G bonds. The hypervariable area examined in the study and modeled in Figure 3 is corresponds to nucleotide positions 237–359.



(A) *Aptostichus atomarius*

(B) *Ryuthela nishihirai*

(C) *Ornithodoros moubata*

(D) *Vaejovis carolianus*

Figure 2.—Proposed secondary structures of a hypervariable region of 16S based on Gutell et al. model (1993) for 4 Arachnid taxa. Solid lines indicate tertiary interaction with strong comparative data and dashed lines indicate those with less support (Gutell 1996). (a) *Aptostichus atomarius* (Mygalomorphae) (b) *Ryuthela nishihirai* (Mesothelae) (c) tick *Ornithodoros moubata* (d) scorpion *Vaejovis carolianus*.

Phylogenetic analysis.—Phylogenetic analyses were performed using PAUP* version 4.0b2a (Swofford 1999) run on a Power Macintosh 6500/275. The phylogenetic signal in the data set was evaluated using the g_1 statistic (Hillis & Huelsenbeck 1992) based on 100,000 random trees generated in PAUP*. All characters were treated as reversible, unordered, and all characters were initially weighted equally. Unambiguous gaps were scored as binary characters. These binary scorings were retained and the individual nucleotide positions from which they were scored were excluded from the analysis. Otherwise, gaps were treated as missing characters.

Heuristic searches were performed using random addition stepwise (1000 replicates) of taxa followed by TBR (tree bisection-reconnection) branch swapping. Branches with a maximum length of zero were collapsed. Measure of branch support is based on decay (Bremer 1988; Donoghue et al. 1992) and bootstrap analyses (Felsenstein 1985). Decay indices were computed using the computer program Autodecay (Eriksson & Wikstrom 1996). Bootstrap values are based on 500 replicates using strict parsimony in PAUP*.

RESULTS

Secondary structure model.—A 503 base pair segment of the 3′ half of 16S was obtained for 6 mygalomorph taxa. Figure 1 shows the proposed secondary structure for the mygalomorph *Aptostichus atomarius* based on the Gutell model. While the mygalomorph model shares substantial physical similarity with the araneomorph and *Drosophila* models, the underlying RNA sequences vary greatly except in some highly conserved regions (Fig. 1). The location of these conserved regions serve as anchor points for establishing the molecule's overall secondary structure. The structural similarity among the models has been maintained through compensatory changes and by slight shifting of structural regions to accommodate nucleotide substitutions.

Structural evolution in the hypervariable region.—Alignment of 16S sequences from the various arachnid taxa sampled revealed a highly variable length of DNA; models of this "hypervariable" region showed marked variation in the size of loops and the length of stems (Fig. 2). Interestingly, bases identified as highly conserved (Buckley et al. 2000) are found adjacent to and even within this region. Evolution in the hypervariable segment of 16S (Fig. 2) reveals an overall trend towards reduction in more advanced arachnids. We will describe this trend moving clockwise through the region (Fig. 2). The models demonstrate extreme variability in loop 1, which varies in length from 9 nucleotides in *Aptostichus* to 30 in *Ornithodoros* (tick). The stem supporting this loop is variable as well, ranging from 3 base pairs in *Aptostichus* and *Heptathela* to 11 base pairs in the tick. The connecting region 2 is short in spiders as it is in humans and *Drosophila* but is longer in *Vaejovis* (scorpion) and the tick than in spiders. Stem 3, which contains the sequence of four G's common to all organisms, is slightly shorter in the spiders than in the tick or the scorpion. Area 4 consists of approximately the same number of nucleotides in the arachnids sampled; the morphological differences result from different amounts of base pairing. Region 5 is maintained by two sets of bonds, which uphold the structural integrity of the stem but permit sufficient freedom for tertiary interactions. The stem and loop of region 6 are most reduced in *Aptostichus* although the "AUU" sequence in the loop is conserved in all arachnids sampled. The importance of this sequence is supported by Buckley et al. (2000), who found it to be conserved throughout insect taxa. Finally, the length of connector 7 is fairly conserved, ranging from 14 nucleotides in *Heptathela* to 20 in the tick.

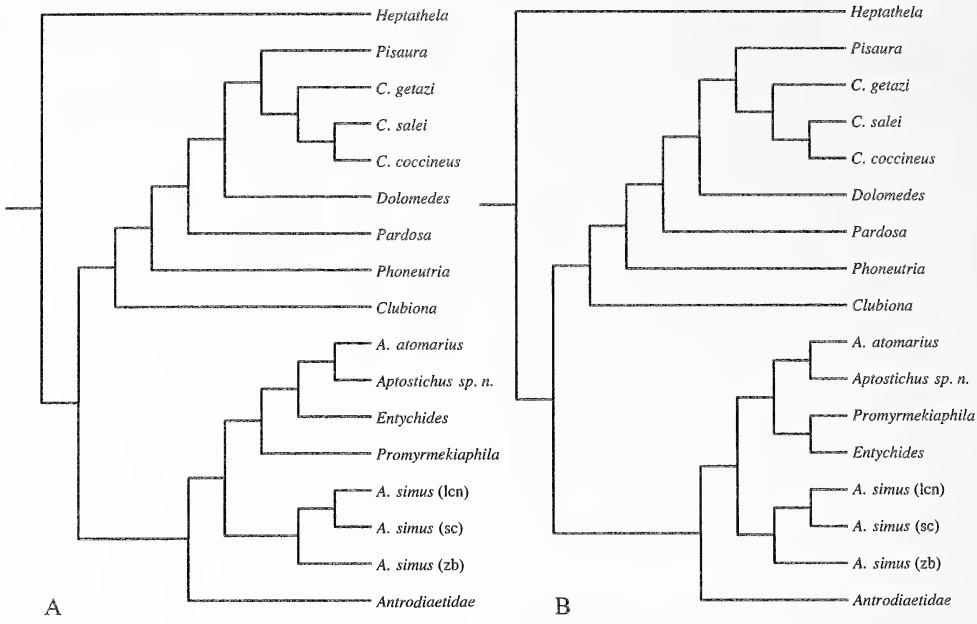
Table 2.—Summary of genetic variability within each structural category.

	Mygalomorphs		Araneomorphs	
Structure	Number of positions	Percent variable	Number of positions	Percent variable
Stems	65	32%	54	24%
Inner loops	62	45%	62	66%
Loops	103	51%	99	46%
Connecting	217	38%	235	32%

Pattern of variation with respect to structure.—Table 2 summarizes the pattern of variation within the 16S molecule for mygalomorphs and araneomorphs. A Wilcoxon Rank Sum Test shows that the variability of each structural class (S, I, L, C) is statistically different for both mygalomorphs ($P < 0.05$) and araneomorphs ($P < 0.0001$).

The mean observed variability of the four structural classes differed from both the small (expected (e) = 0.29, $X^2 = 40.34$, $P < 0.005$) and large ($e = 0.33$, $X^2 = 26.93$, $P < 0.005$) random blocks for the araneomorphs. However, the mean variability values for mygalomorphs were not statistically distinct from the random model (small blocks: $e = 0.42$, $X^2 = 4.49$, $P > 0.10$; large blocks: $e = 0.43$, $X^2 = 4.68$, $P > 0.10$).

Phylogeny reconstruction.—We consider the phylogenetic signal in this data set to be significant ($g_1 = -0.55$, $P < 0.01$). A strict parsimony analysis with all positions weighted equally resulted in two equally parsimonious trees (Figs. 3a & b), 719 steps in length (CI = 0.61, RI = 0.66). Subsequent analyses with loop and inner loop positions first downweighted to 0.20 and then excluded each resulted in one most parsimonious tree with slightly improved CI and RI values (Fig. 4).



Figures 3 A, B.—Two equally parsimonous trees based on 16S sequences in which all positions are weighted equally, both 719 steps in length (CI = 0.61, RI = 0.66). "C." stands for the genus *Cupiennius* and "A." for the genus *Aptostichus*. Locations for *A. simus* populations are Leo Carillo State Beach, Los Angeles County, CA (lcn), Sycamore Cove Beach, Ventura County CA (sc) and Zuma Beach County Park, Los Angeles County, CA (zb).

DISCUSSION

Secondary structure.—With the exception of a few hypervariable regions of the molecule, the mygalomorph secondary structure bears close resemblance to those structures proposed for prokaryotes (Gutell 1996; Larsen 1992), insects (Buckley et al. 2000), and araneomorphs (Huber et al. 1993). This supports the findings of Wheeler & Honeycutt (1988), which demonstrated that Darwinian selection must be operating strongly on these genes to maintain the functional aspects of secondary structure.

The alignment of DNA sequence is computationally difficult (Swofford et al. 1996: Slowinski 1998). Comparison of the mygalomorph model to other arthropod secondary structures facilitated the identification of conserved areas, which were integral to improving the alignment (Buckley et al 2000). Ribosomal RNA sequences add another level of complexity to the problem of sequence alignment because nucleotide site position alignment is determined by secondary structure position homology. Sequence alignments that account for true molecular structural homology by identifying conserved regions are most likely to reflect true homology and thus correct gene phylogeny, a consideration that may not be reflected in alignment approaches that invoke overall similarity (e.g., Higgins et al. 1996) or concurrent optimizations of alignment and phylogenetic inference (e.g., Wheeler & Gladstein 1994).

Trends in secondary structure evolution in the hypervariable region.—Examination of the hypervariable region (Fig. 2) suggests a general trend toward the reduction of stems and loops in Araneae. The *Aptostichus* and *Heptathela* models exhibit a large deletion in the stem and loop of region 1 (Fig. 2), similar to that observed by Masta (2000) in *Habronattus oregonensis* (Peckham & Peckham 1888). The size of region 1 in the scorpion and the tick (39 and 53 nucleotides, respectively) is an intermediate between *Drosophila* (55 nucleotides) and *Aptostichus* (15 nucleotides). This suggests a pattern of evolution towards reduction of region 1, a possible synapomorphy of spiders. However, based on Wheeler & Hayashi's (1998) chelicerate phylogeny, additional 16S sequence data are re-

quired for at least palpigrades, amblypygids, and schizomids before this can be stated unequivocally. The main exceptions to this reductionary trend are those areas involved in tertiary interactions, such as region 5 and connecting region 7 (Fig. 2). The size of these areas varies little from *Drosophila* to humans to arachnids.

The extreme variability of region 1 in spiders may be due to its position in the tertiary structure of the fully-formed ribosome. When addressing why a certain segment of a ribosomal subunit is more variable than others, Simon et al. (1994) proposed that it is important to consider the position of the segment in the molecule. Peripheral secondary structure elements tend to be more variable than those on the interior and more frequently undergo modification or elimination. The hypervariabililty of this portion of 16S (Fig. 2) suggests that it is probably located on the periphery of the molecule.

Pattern of variation with respect to structure.—Within the Mygalomorphae and Araneomorphae, both the stem (S) and connecting (C) regions exhibited lower variability than the loops (I, L), although this difference was most distinct in the araneomorphs (Table 2). Because stems must base pair to maintain their integrity, changes that disrupt base pairing along the stem will be less likely to occur. Connecting regions are probably more conserved because they have a vital function in maintaining the spatial arrangement of the molecule. Loops are less constrained as changes in their sequence will not interrupt base pairing and at most will threaten tertiary interactions. Additionally, changes in length of the loops will have a small effect on the overall form of the molecule. This disparity in variability between stems and loops is different from what has been observed for other ribosomal RNA molecules. Wheeler & Honeycutt (1988) found stems to be more variable than loops for 5.8S rRNA, the small nuclear subunit (SSU). They suggest that this was due to the compensatory nature of nucleotide base changes in the stems. Mutations in one base pair would result in a selection pressure for changes in the other, causing stem nucleotide pairs to evolve in concert.

Effects of differential weighting of structural regions.—The results of this study demonstrate the importance of considering 16S rRNA secondary structure for phylogenetic reconstruction. Differentially weighting segments of the 16S rRNA based on their structural properties prevents the overemphasis of homoplasic nucleotide positions. This was most evident for the mygalomorph taxa. Down-weighting the variable loops and inner loops improved the phylogenetic tree, which recovered *Aptostichus* as a monophyletic group (47), a grouping supported by combined analyses of morphological and molecular data (Bond 1999; Bond & Opell 2002). This ability to fine tune a data set, omitting or differentially weighting hypervariable regions, may allow 16S sequence data to be applied more broadly. At the population level, highly variable loops would provide phylogenetic signal while those same loops could be disregarded for comparison of intermediate or very disparate taxa in favor of more conserved stems or connecting regions.

Because this study utilizes only the 3′ half of the 16S, application of our differential weighting scheme may require adjustment when considering the entire molecule. Simon (1991) pointed out that smaller short range stems (terminal stems) vary substantially more than long range stems (supporting stems) and can evolve as rapidly as some loops. Simon (1991) suggested that, if differential weighting were employed, these two types of stems should be distinguished and the rapidly evolving shorter stems should be down-weighted. In the segment of 16S used in this study, there were 16 short range stems and only one strand of two long range stems. Therefore, the mean variability for stems could be considered representative of short-range stems. Perhaps, if the system of differential weighting used in this study were employed on a longer sequence of LSU rRNA, the two stem types would have to be distinguished.

Summary.—The majority of sequence based phylogenetic studies rely solely on DNA sequence alignment algorithms and weighting schemes based on nucleotide compositions. Not surprisingly, this study demonstrates that greater understanding of the processes underlying nucleotide sequence evolution will increase the likelihood of recovering the correct phylogenetic relationships. We show that at very "deep" phylogenetic levels gross secondary structure, the

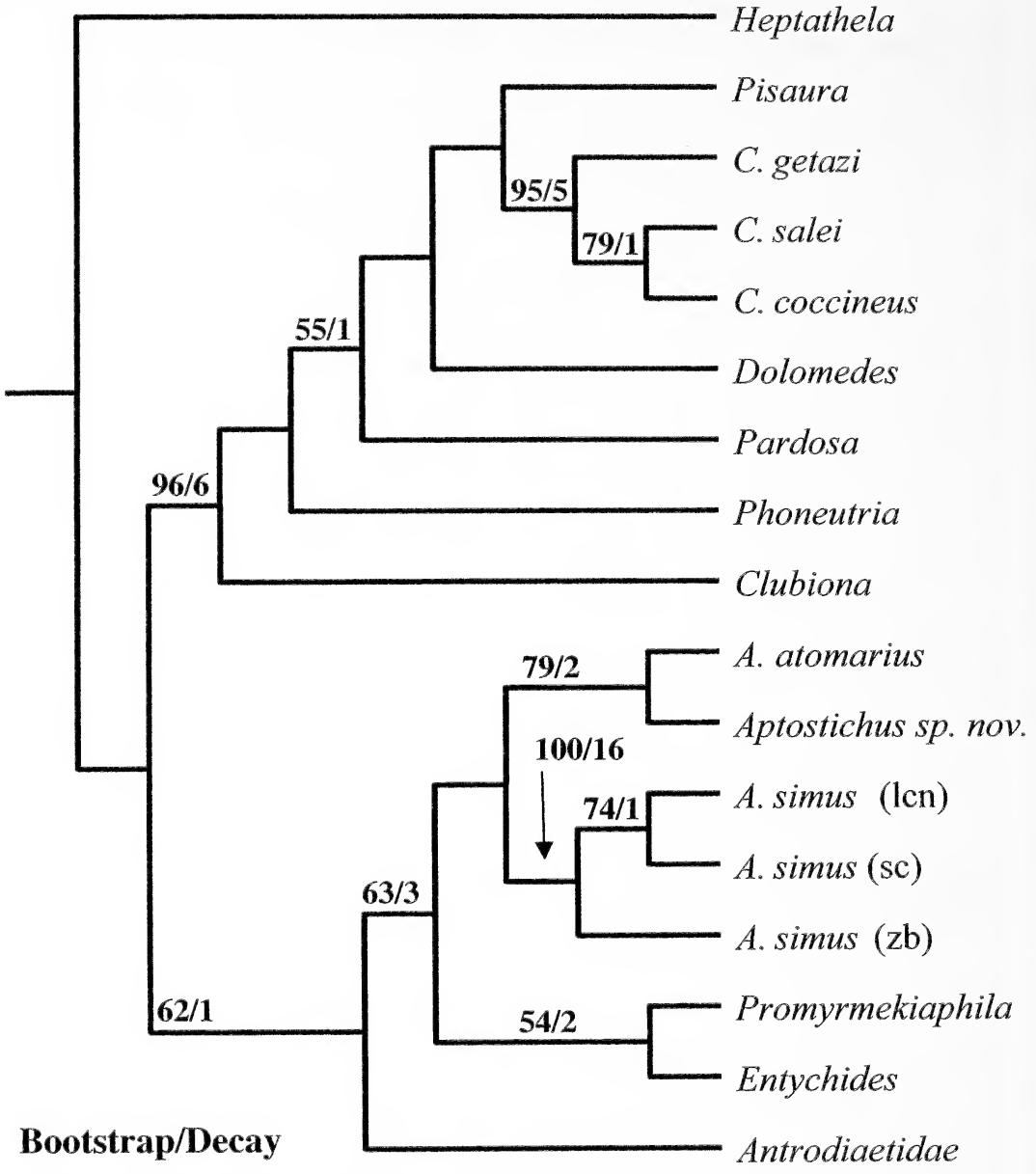


Figure 4.—Tree produced when loop and inner loop positions of 16S are down-weighted to 0.20 (520.8 steps, CI = 0.63, RI = 0.69) and when loops and inner loops were excluded (471 steps, CI = 0.63, RI = 0.70). Bootstrap values and decay indices refer to the tree with loops downweighted.

morphology of the molecule, may very well contain phylogenetic information useful in reconstructing arachnid relationships. At more intermediate phylogenetic levels (inter-familial) we show that by down-weighting loop nucleotides phylogenetic signal may be improved. Although the conclusions drawn here may be limited to arachnid studies, the statistical approach employed may be useful for studies of secondary structure in other groups.

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BOTHRIURUS JESUITA, A NEW SCORPION SPECIES FROM NORTHEASTERN ARGENTINA (SCORPIONES, BOTHRIURIDAE)

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ABSTRACT. The new species *Bothriurus jesuita* is described. This species belongs to the *bonariensis* species group and is closely related to *Bothriurus chacoensis* Maury & Acosta 1993 from which it can be distinguished by its thicker and taller chela and because of it is almost 30% larger. It can be distinguished from *Bothriurus bonariensis* (C.L. Koch 1842) because it has an apical filament on the basal lobe of the right hemispermatophore and because the frontal ridge reaches the frontal fold. *Bothriurus jesuita* has been collected in the northern region of Corrientes Province and in Misiones Province in an area that belongs to the "Paranaense" Phytogeographic Province.

RESUMEN. En el presente trabajo se describe a *Bothriurus jesuita* sp. nov., esta especie pertenece al grupo *bonariensis* y se encuentra muy relacionada con *Bothriurus chacoensis* Maury y Acosta 1993; puede diferenciarse de ésta por poseer una pinza más alta y robusta, y por ser casi un 30% más grande. Puede diferenciarse de *Bothriurus bonariensis* (C.L. Koch 1842) por poseer un filamento en el lóbulo basal del hemiespermatóforo derecho, y porque la cresta frontal de la lámina distal llega hasta el repliegue frontal. *Bothriurus jesuita* sólo ha sido colectada en el norte de la provincia de Corrientes y en la provincia de Misiones, en un área correspondiente con la provincia fitogeográfica Paranaense.

Keywords: *Bothriurus*, Neotropics, scorpion, taxonomy.

The genus *Bothriurus* is the most diverse in the family Bothriuridae. To facilitate identification of species in the genus, it was divided into species groups (Maury 1973, 1979, 1984), one of which is the *bonariensis* species group (Maury 1979). The distinctive characteristics of this group are as follows: chela trichobothrium esb forms a triangle with eb 2 and eb 3, hemispermatophore lamina very well developed, straight with a frontal ridge, chelicerae with a single subdistal tooth, ventrolateral and transverse carinae forming an arc in the distal third of the fifth metasomal segment, males metasomal gland placed in a very conspicuous depression on the dorsal face of the telson (Maury & Acosta 1993; Acosta & Maury 1998).

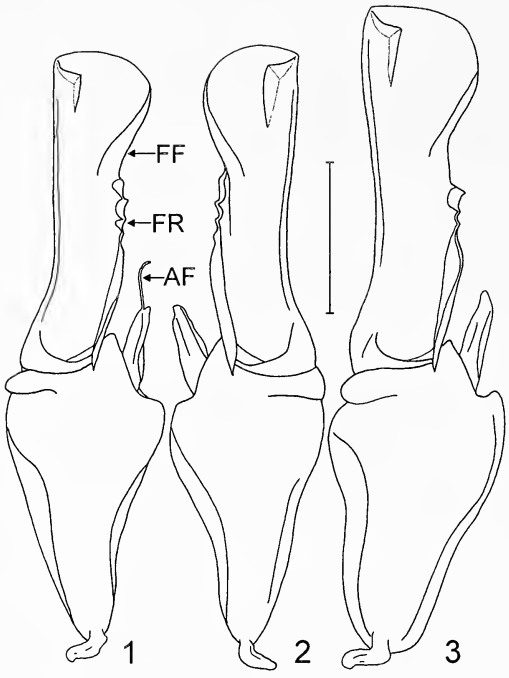
Currently the *bonariensis* group contains only two species: *B. bonariensis* (C.L. Koch 1842) and *B. chacoensis* Maury & Acosta 1993. *Bothriurus jesuita*, a new species from the *bonariensis* group, is herein described. This species was first recognized as distinct by Dr. San Martín; all the specimens examined for this paper were labelled by him as a new species: *Bothriurus vianai* (nomen nudum, in schedula). Maury & Acosta (1993) mention the presence of this new species from the Argentinian Mesopotamia, but they never attempted to describe it.

Bothriurus jesuita is the fourth species recorded for the Misiones scorpiological area (Acosta & Maury 1998), the other species are: *Tityus bahiensis* (Perty 1833), *Bothriurus moojeni* Mello Leitão 1945 and *Ananteris balzanii* Thorell 1891, although the presence of the last species in the area has to be confirmed (Mello Leitão 1945; Lourenço 1993; Ojanguren Affilastro & Vezzani 2001).

A map of the distribution of the species of the *bonariensis* group in Argentina is provided. All the localities given in this map belong to the bibliography cited in this paper, except for the new records of *Bothriurus jesuita*.

METHODS

Terminology of the structures of the hemispermatophore follows Maury (1973) and Maury



Figures 1–3.—*Bothriurus jesuita* new species. 1. Right hemispermatophore, dorsal aspect; 2. Left hemispermatophore, dorsal aspect; 3. *Bothriurus bonariensis*, right hemispermatophore, dorsal aspect. Abbreviations: AF = apical filament; FR = frontal ridge; FF = frontal fold. Scale bar = 1 mm.

& Acosta (1993). Trichobothrial terminology follows Vachon (1974). Terminology of the telson gland follows Maury & Acosta (1993). Terminology of the Phytogeographic Provinces follows Cabrera & Willink (1980). Terminology of the Scorpiological Areas follows Acosta & Maury (1998). Terminology of the metasomal carinae follows Stahnke (1970). Abbreviations for collections are as follows: MACN-Ar = Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", National Arachnological Collection (Cristina Scioscia). All measurements are in mm, and were taken using an ocular micrometer. Illustrations were produced using a stereomicroscope and camera lucida. The hemispermatophores were dissected from surrounding tissues and observed in 80% ethanol.

***Bothriurus jesuita*, new species**
Figs. 1, 2, 5–10, 12–16

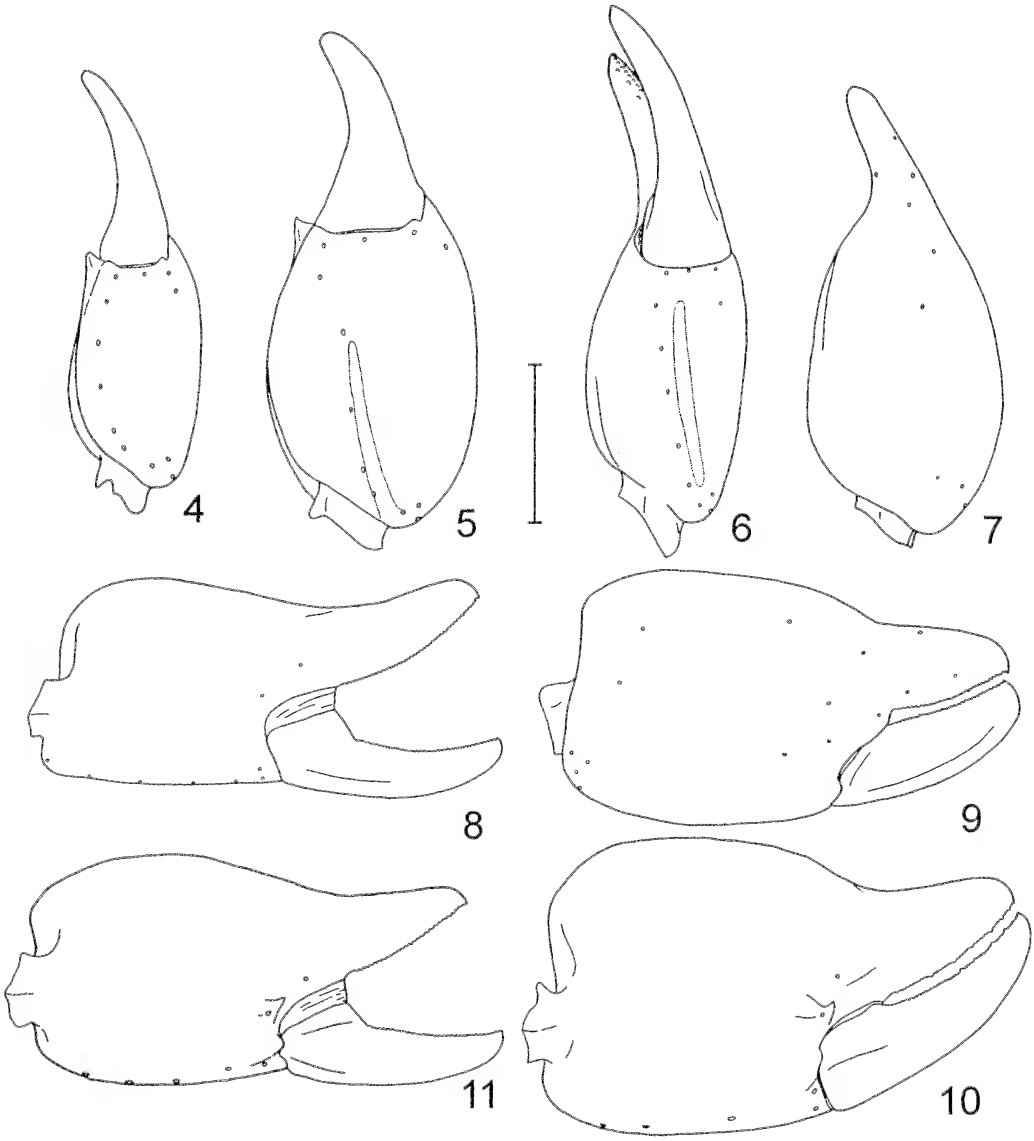
Bothriurus vianai: San Martín (nomen nudum, in schedula).

Bothriurus bonariensis (C.L. Koch): Maury 1973: 368, 369, map (in part.); Maury 1979: 708, 715, fig. 5 (in part).

Bothriurus sp: Maury & Acosta 1993: 114, 118.

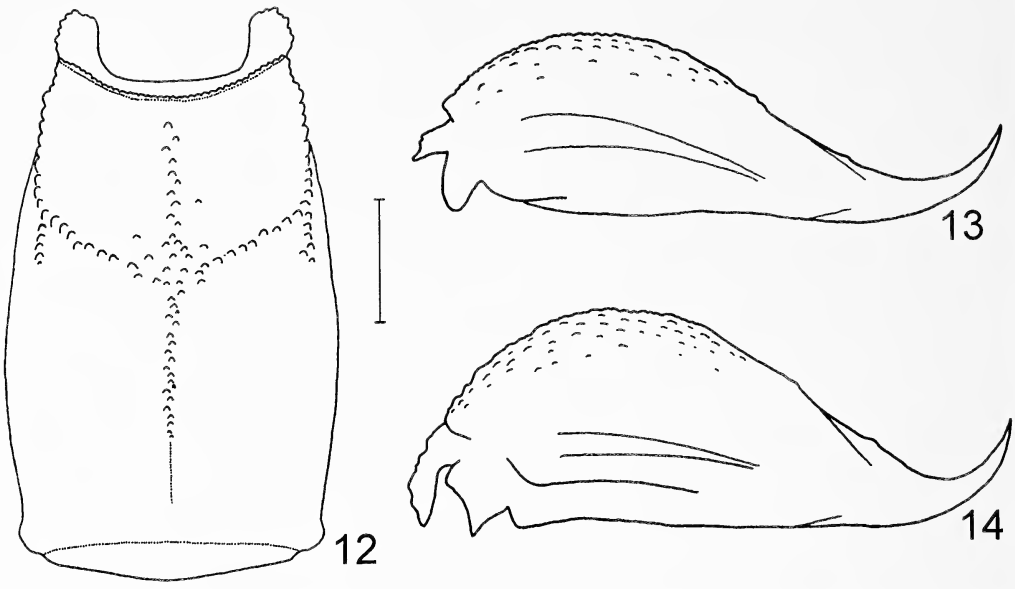
Type data.—Holotype male, ARGENTINA: *Misiones Province,* Loreto (27°19′S, 55°31′W), 1936, Ogloblin coll. (MACN-Ar 10048). Paratypes: *Misiones Province*: San Ignacio (27°16′S, 55°31′W), 1 ♂, December 1948, Biraben coll. (MACN-Ar 10049); 1 ♂, December 1948, Biraben coll. (MACN-Ar 10052); San Javier (27°52′S, 55°7′W), 2 juveniles, December 1948, Biraben coll. (MACN-Ar 10050); Santo Pipó (27°7′S, 55°31′W), 1 ♂, 1 ♀, December 1951, Foenter coll. (MACN-Ar 10051); Santa Ana (27°22′S, 55°34′W), 1 ♂, Llamas coll. (MACN-Ar 10053); 1 juvenile, Llamas coll. (MACN-Ar 10071); 1 ♂, March 1901, Llamas coll. (MACN-Ar 10057); San Juan (27°46′S, 55°30′W), 1 ♂, 3 August 1924, Gómez coll. (MACN-Ar 10054); Loreto (27°19′S, 55°31′W), 2 juveniles, 15–20 December 1932, Ogloblin coll. (MACN-Ar 10055); 1 ♂, February 1956, Sánchez de Bustamante coll. (MACN-Ar 10063); 1 ♂, 8 January 1933, (MACN-Ar 10059); 1 ♂, 10 February 1937, (MACN-Ar 10060); Puerto Bemberg (Urugua-í, 25°55′S, 54°36′W), 1 ♀, 1 juvenile, 25 November 1948, (MACN-Ar 10056); San José (27°46′S, 55°46′W), 3 juveniles, December 1948, Biraben coll. (MACN-Ar 10058); Apóstoles (27°53′S, 55°46′W), 1 ♂, 1 juvenile, March 1935, Castelli coll. (MACN-Ar 10061); Pindapoy (San Jose, 27°46′S, 55°46′W), 1 ♂, 1 juvenile, 12 January 1942, Williner coll. (MACN-Ar 10070); Santa María (27°55′S, 55°22′W), 3 ♂, December 1943, Viana coll. (MACN-Ar 10062); 1 ♂, November 1952, Viana coll. (MACN-Ar 10064); 1 ♂, January 1964, Viana coll. (MACN-Ar 10065); 1 ♂, March 1945, Viana coll. (MACN-Ar 10066); 1♂, December 1948, Viana coll. (MACN-Ar 10067). *Province of Corrientes*: Manantiales (27°56′S, 58°7′W), 1 ♂, May 1947, Apostol coll. (MACN-Ar 10068); Apipé (27°31′S, 56°43‘′W), 1 ♂, December 1945, Hanke coll. (MACN-Ar 10069).

Etymology.—The specific epithet comes from the Spanish name of the Jesuit catholic order. This species has been mainly collected near the ruins of the missions that the Jesuit order constructed in the XVII and XVIII centuries.



Figures 4–11.—*Bothriurus jesuita* new species, 5. Left chela, male, ventral aspect; 6. Left chela, female, ventral aspect; 7: Right chela, male, dorsal aspect; 8. Left chela, female, prolateral aspect; 9. Right chela, male, retrolateral aspect; 10. Left chela, male, prolateral aspect. 4, 11: *Bothriurus chacoensis*, 4. Left chela, male, ventral aspect; 11. left chela, male, prolateral aspect. Scale bar = 1 mm.

Diagnosis.—*Bothriurus jesuita* can be distinguished from *B. bonariensis* by having an apical filament on the basal lobe of the right hemispermatophore (Fig. 1), that is lacking in the left one (Fig. 2), and by the frontal ridge reaching the frontal fold, whereas in *B. bonariensis* it does not (Fig. 3). *Bothriurus jesuita* is morphologically most similar to *B. chacoensis*; both species share the particular shape of their hemispermatophores, but *Bothriurus jesuita* has a wider and higher pedipalp chela (Figs. 4–11); chela length/chela width: 2.6–3.02 (n = 25; mean = 2.74) in *B. chacoensis* males, 3.12–3.36 (n = 25; mean = 3.24) in females; 2.25–2.56 (n = 18; mean = 2.47) in *B. jesuita* males, 2.89–3.01 (n = 3; mean = 2.93) in females; chela length/chela height: 1.84–2.22 (n = 25; mean = 1.97) in *B. chacoensis* males,



Figures 12–14.—*Bothriurus jesuita* new species, 12. Fifth caudal segment, ventral aspect; 13. Telson, male, lateral aspect; 14. Telson, female, lateral aspect. Scale bar = 1 mm.

2.33–2.52 (n = 25; mean = 2.4) in females; 1.68–1.8 (n = 18; mean = 1.76) in *B. jesuita* males, 2.15–2.24 (n = 3; mean = 2.21) in females. Although in the extremes of variation the ratios may overlap, no specimens have been found where both ratios overlap (Fig. 15), so to be certain of the identification of the species both ratios must be used. *Bothriurus bonariensis* ratios are similar to those of *B. jesuita*, but in some specimens they overlap with those of *B. chacoensis* (Fig. 15); *B. bonariensis* chela length/chela height ratio: males 1.68–1.85 (n = 20; mean = 1.76), females 1.80–1.98 (n = 20; mean = 1.96); length/width ratio: males 2.36–2.66 (n = 20; mean = 2.50), females 2.97–3.20 (n = 20; mean = 3.06). *Bothriurus jesuita* is approximately 30% longer than *B. chacoensis*; *B. jesuita*: males 39–47 mm (n = 18; mean = 44.7), females 52–59 mm (n = 3; mean = 55.3); *B. chacoensis*: males 28–35 mm (n = 25; mean = 31.5), females 30–36 mm (n = 25; mean = 33.8). *Bothriurus jesuita* has a darker and more uniform color pattern than *B. chacoensis*.

Description.—*Coloration:* Carapace, pedipalps, tergites and metasoma: base color dusky brown with moderately dense variegated darker pattern; chelicerae and pectines brown-yellow with underlying dusky pattern; sternites dark brown with some yellow spots; legs dark brown with some yellow spots in coxa and trochanter; telson dark brown except the metasomal gland in males that is light yellow.

Morphology: Measurements of male holotype and a female paratype (MACN-Ar 10051) in table 1. Prosoma: carapace: tegument finely granular, front border with a slight notch, median ocular tubercle located in the center of the carapace, eyes one diameter apart, postocular furrow and lateral sulcus moderately deep; chelicerae with a single subdistal tooth. Mesosoma: tergites I to VI finely granular, VII finely granular with two posterolateral carinae; sternites smooth. Metasoma: segment I: dorsosubmedian carina represented only by 4 or 5 coarse granules in the second half of the segment, dorsolateral carinae present only in the second part of the segment, median lateral carinae present only in the distal third of the segment; segment II and III: dorsosubmedian and dorsolateral carinae like in segment I, median lateral carina represented by some tiny granules at the end of the segment; segment IV: dorsosubmedian carina like segment I, dorsolateral and median lateral carinae absent; segment V: ventrolateral carinae in the distal third, forming an arc with the transverse carinae which surrounds some scat-

Table 1.—*Bothriurus jesuita,* measurements (mm) and number of pectinal teeth of the holotype male and a female paratype.

	Male holotype	Female paratype
Total length	42.76	52.28
Prosoma, length	4.85	5.66
Prosoma, anterior width	3.31	4.53
Prosoma, posterior width	5.82	7.11
Mesosoma, total length	11.41	18.58
Metasoma, total length	26.5	28.04
Metasomal segment I, length	2.51	3.39
Metasomal segment I, width	3.96	4.28
Metasomal segment I, height	2.83	3.56
Metasomal segment II, length	3.10	3.56
Metasomal segment II, width	3.88	4.12
Metasomal segment II, height	2.99	3.47
Metasomal segment III, length	3.47	3.88
Metasomal segment III, width	3.88	4.04
Metasomal segment III, height	3.23	3.39
Metasomal segment IV, length	4.36	3.64
Metasomal segment IV, width	3.79	4.04
Metasomal segment IV, height	3.31	3.72
Metasomal segment V, length	6.06	6.71
Metasomal segment V, width	3.72	4.04
Metasomal segment V, height	2.99	3.39
Telson, length	7.00	6.86
Vesicle, length	4.12	5.17
Vesicle, width	2.99	3.39
Vesicle, height	2.18	2.51
Aculeus, length	2.18	1.69
Pedipalp, total length	14.54	17.69
Femur, length	3.56	4.20
Femur, width	1.69	1.86
Patella, length	3.79	4.20
Patella, width	1.62	1.94
Chela, length	7.19	9.29
Chela, width	2.91	2.75
Chela, height	4.12	3.79
Movable finger, length	3.79	4.44
Number of pectinal teeth	22–22	18–18

tered granules, ventromedian carina occupies the whole segment except a small area near the front border (Fig. 12). Telson: tegument finely granular, vesicle dorsoventrally compressed (Fig. 13), aculeus short, in females the vesicle is more globose and the aculeus is shorter (Fig. 14), in males the metasomal gland is placed dorsally in a very conspicuous pit. Pedipalps: femur granulated, ventrointernal and dorsointernal carinae poorly developed, patella smooth, chela high and thick, with a ventroexternal carina, apophysis of males scarcely developed, short fingers, trichobothrial pattern typical of the bonariensis group: neobothriotaxic major type C: femur with 3 trichobothria: 1 d, 1 i and 1 e; patella with 3 v trichobothria and 13 trichobothria on its external face: 3 et, 1 est, 2 em, 2 esb and 5 eb; chela with 12 trichobothria on its prolateral face: 1 est, 2 et, 5 v, 1 esb and 3 eb; no intraspecific variation has been observed in this character; chela trichobothrium esb forms a triangle with eb 2 and eb 3. Legs: smooth tegument; ventrosubmedian spiniform setae of the telotarsi: telotarsus I: 1+1, telotarsus II: 2+2, telotarsi III & IV: 3+3; no intraspecific variation has been observed in this character. Hemispermatophore: distal lamina very well

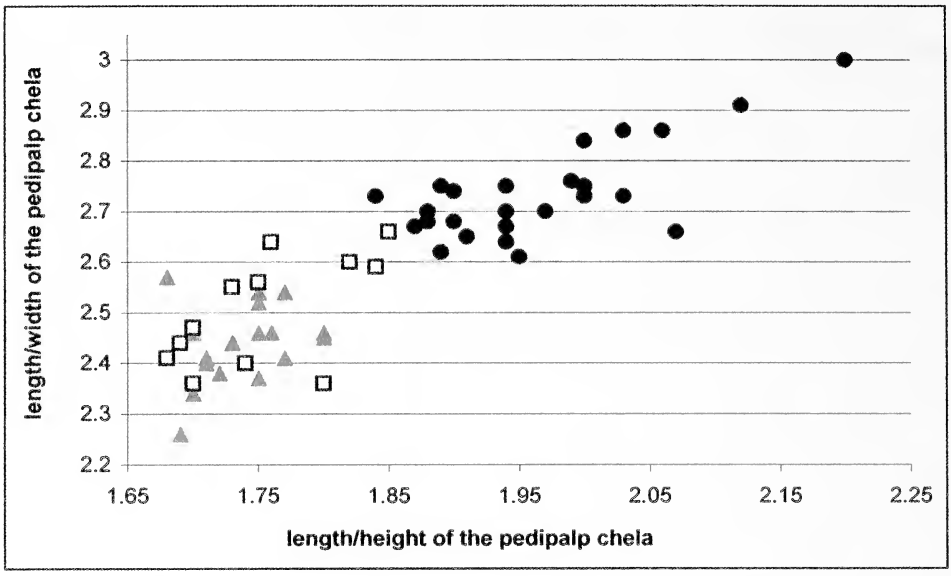


Figure 15.—Length/height ratio of the pedipalpal chela, against length/width ratio of the pedipalp chela; males of *Bothriurus jesuita* (grey triangles), males of *Bothriurus chacoensis* (black circles), and males of *Bothriurus bonariensis* (white squares).

developed, straight with a frontal ridge that reaches the frontal fold; there is an apical filament on the basal lobe of the right hemispermatophore that is lacking in the left (Figs. 1 & 2).

Variation.—Total length in males, 39–47 mm (n = 18; mean = 44.7), in females 52–59 mm (n = 3; mean = 55.3). Number of pectinal teeth, in males: 20–23 (n = 18; median = 21), and in the 3 females examined 18. Chela length/chela width: 2.25–2.56 (n = 18; mean = 2.47) in males, 2.89–3.01 (n = 3; mean = 2.93) in females; chela length/chela height: 1.68–1.8 in males (n = 18; mean = 1.76), 2.15–2.24 (n = 3; mean = 2.21) in females.

Distribution.—*Bothriurus jesuita* has been collected in Argentina, in the northern part of Corrientes Province and in Misiones Province (Fig. 16). This area belongs to the "Paranaense" Phytogeographic Province, and to the Misiones Scorpiological Area.

It is interesting to note that the distribution of the species of the bonariensis group matches almost exactly three different Phytogeographic Provinces; *B. chacoensis* is found almost exclusively in the "Chaqueña" Province with a very slight extension into the "Espinal" Province (Maury & Acosta 1993; Acosta & Maury 1998); *B. bonariensis* is found in the "Pampeana" Province, although it has also been found in the "Espinal" (Maury 1973; Maury 1979, 1986; Acosta & Rosso de Ferradás 1996; Acosta & Maury 1998); and *B. jesuita*, the most restricted species, has been found so far only in the "Paranaense" Province.

In Manantiales, in the northern region of Corrientes Province, several specimens of *B. chacoensis* have been found, together with a specimen of *B. jesuita*. Since this locality lies at the border of the "Paranaense" and "Chaqueña" Phytogeographic Provinces, it is not strange to find both species in sympatry. It is very probable that *B. jesuita* is also present in southern Brazil and eastern Paraguay, although we have not had access to any specimen that confirms this distribution.

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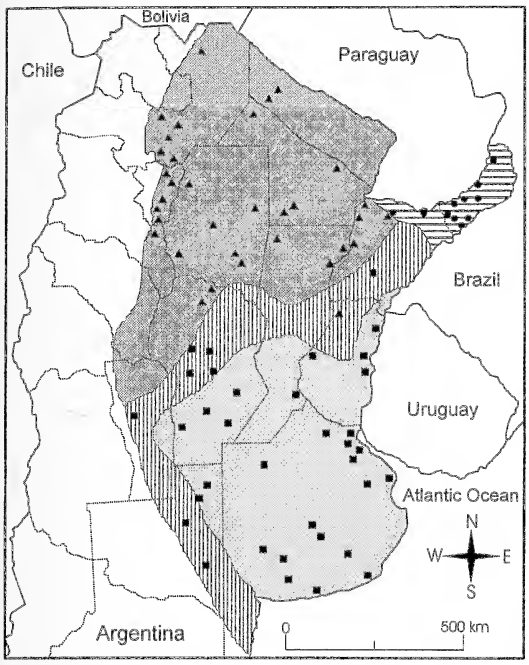

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Figure 16.—Distribution of the species of the *bonariensis* group in Argentina, and the Phytogeographic Provinces where they have been collected. Black circles: *Bothriurus jesuita*, black triangles: *Bothriurus chacoensis*, black squares: *Bothriurus bonariensis*, hatched horizontal: "Paranaense" Phytogeographic Province; hatched vertical: "Espinal" Phytogeographic Province; dark grey: "Chaqueña" Phytogeographic Province; light grey: "Pampeana" Phytogeographic Province.

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MARQUESAN SPIDERS OF THE GENUS *TETRAGNATHA* (ARANEAE, TETRAGNATHIDAE)

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ABSTRACT. This study revises the status of knowledge of the spider fauna of the Marquesas Islands in French Polynesia. In particular, the genus *Tetragnatha* was noticeable for its poor representation in the Marquesas Islands by comparison with the large radiation in the yet more remote Polynesian archipelago of the Hawaiian Islands. Expeditions were conducted to determine whether *Tetragnatha* was indeed poorly represented in the Marquesas Islands, as the literature would suggest. In addition, specimens were studied from historical collections from this archipelago. The results indicate that the islands do indeed have a number of endemic *Tetragnatha*, and the genus does appear to have undergone adaptive radiation, although not nearly on the same scale as in the Hawaiian Islands. Results indicate that: (1) in addition to *T. marquesiana* Berland there are four new species, described here, each of which are endemic to the islands. *Tetragnatha marquesiana* is widespread in the northern islands, including Nuku Hiva. There are two additional species on Nuku Hiva: *T. punua* and *T. oomua*. Two new species are described from the southern islands of Hiva Oa (*T. kapua*) and Tahuata (*T. tahuata*). *Tetragnatha kapua* from Hiva Oa appears to be related to *T. marquesiana*. (2) *Tetragnatha macilenta* L. Koch does not occur on these islands. Reports of its widespread distribution through the Pacific can only be substantiated as far as the Society Islands. (3) *Tetragnatha nitens* (Audouin), which may not be indigenous, occurs in disturbed areas at high elevations in Nuku Hiva. In total, there are six species of *Tetragnatha* in the Marquesas Islands.

Keywords: Marquesas, descriptions, Pacific, biogeography

The Marquesas is a remote archipelago consisting of eight high (> 500 m) islands (Fig. 1), situated 150 km from the nearest island group (Society Islands), and 7300 km from the nearest continental land mass (South America; approx. 7500 km from Australia). In common with the other remote Polynesian archipelagoes of the Hawaiian and Society islands, the Marquesas Islands are all volcanic in origin, and formed as volcanic hot spots. All three archipelagoes exhibit a chronological arrangement of islands, which in the Marquesas ranges from Nuku Hiva, the oldest in the north at 3.7 myrs, to Fatu Hiva, the youngest in the south at 1.4 myrs. In addition to the geological similarity there also appear to be some elements of the indigenous arthropod fauna that are held in common across all three archipelagoes (Meyrick 1935).

To date, knowledge of the spider fauna of the Marquesas Islands has shown little in common with the Hawaiian Islands. Unlike the Society Islands, there have been fairly extensive collections made of spiders in the Marquesas, largely through the efforts of Guillaume LeBronnec, a naturalist from France who lived in the Marquesas. LeBronnec collected arthropods for the Pacific Entomological Survey, an effort mounted by Adamson and Mumford (Adamson 1939), initially through the University of California at Berkeley, and subsequently through the Bishop Museum in Honolulu. The spiders collected through this survey were sent to L. Berland at the Muséum National d'Histoire Naturelle in Paris. Berland (1934) described the fauna of the Marquesas as follows (in translation): "Until present, our knowledge of the spiders was summarized in a short note which I published in 1927 in the Bulletin of the Museum, and I announced 4 species sent by P. Simeon Delmas, of Taiohae: 3 of them were cosmopolitan; and I wondered in conclusion if this archipelago had a good endemic spider fauna. But I had very recently good fortune to be entrusted with abundant material collected in the Marquesas by Mr. Mumford and Mr. Adamson, of the Pacific Entomological Survey, likewise by Mr. LeBronnec and Mr. Tauraa; . . . We now know 38 species, with a coefficient of endemism of 42%, ... making the Marquesas similar to other Polynesian islands.

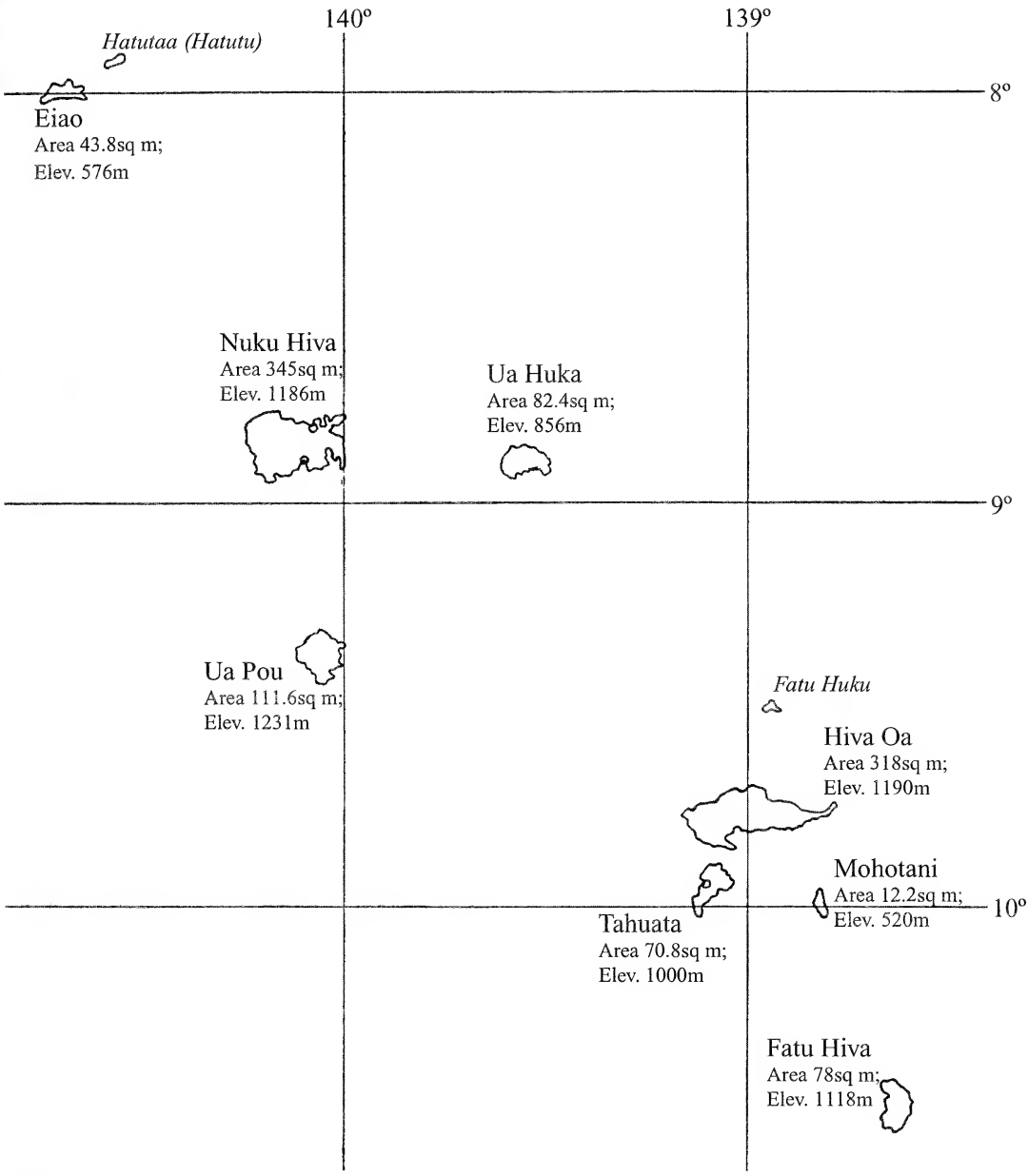


Figure 1.—Map of the Marquesas islands. Those in black are high islands, in gray outline are atolls. Area and elevation are given for the high islands.

This pleasing result is due to the method employed by Adamson and Mumford: not limiting themselves to the collections made in the coastal zone, where there has been considerable deforestation due to cattle imports, they focussed their search on the mountainous and inaccessible interior of each island, where the indigenous fauna has had the most chance to be preserved without alteration. The Polynesian affinities are marked in a certain number of species that one finds in nearby archipelagoes, ...[and] seems to be an invaluable witness of a common origin of all these archipelagoes. Moreover one finds some species which show affinities not only with Polynesia, but also with the more remote areas of the Pacific. . . . Certain spiders have affinities from farther away: *Tetragnatha nitens*, a Med-

iterranean species, is found in Asia minor, India, Malaysia, up to the Marquesas. Finally one recognizes a rather unexpected case: that of a Hawaiian affinity. Mumford and Adamson have told me that this affinity appeared in certain Hemiptera-Homoptera. I have also stated very clearly that the spiders of the genus *Sandalodes* . . . which are represented largely in Hawaii, are also diverse in the Marquesas, with six species, all endemic except *S. calvus* . . . But this is the only Hawaiian affinity which is very clear, and in general the groups which characterize Hawaii by their number: *Tetragnatha*, thomisids, etc, are not found in same abundance in the Marquesas."

One of Berland's conclusions was that, because many of the species that he received from the islands were widespread, there was evidence for a common origin of these archipelagoes. This interpretation was based on a widespread belief at that time that the remote Polynesian islands were once part of a "supercontinent". We now know this to be incorrect and that the islands were formed independently. Moreover, as P.A. Buxton notes in response to Berland's conclusion (as a footnote, p. 39, Berland 1929): "We must not forget that the primitive Polynesians traveled and raided in great canoes, which carried as many as a hundred men, and were provisioned for ocean voyages . . . . We must therefore assume that some of the insects and other arthropods which are domestic were introduced by man many centuries before Europeans entered the Pacific." In a slightly more recent publication, Berland (1935a) wrote (in translation): "The islands include a littoral zone, where one finds mostly cosmopolitans and . . . Polynesian species, but the recent collections of LeBronnec have made known a very interesting fauna, confined to the interior of island and to a certain altitude, several species not being found below 1000 m. It is there that the majority of endemics exist. Comparison between these faunas . . . is currently impossible because the high summits remain the most poorly known of any place on the surface of the Earth". This latter summary is a better reflection of the status of knowledge of the spider fauna of the Marquesas to date.

The current study set out to reassess the distribution of *Tetragnatha* in the Marquesas Islands, and determine whether the lack of representation was due to insufficient collecting, or whether it represented a real paucity of species. I have now collected on Nuku Hiva, Hiva Oa, and Tahuata. I have also examined specimens collected recently by Ron Englund (Bishop Museum) from Ua Huka and Tahuata in October 1999. In addition, I have examined historical collections at the Muséum National d'Histoire Naturelle, Paris (MNHN), Museum für Naturkunde der Humboldt-Universität, Berlin, the Natural History Museum, London, and the Bishop Museum, Honolulu (BPBM).

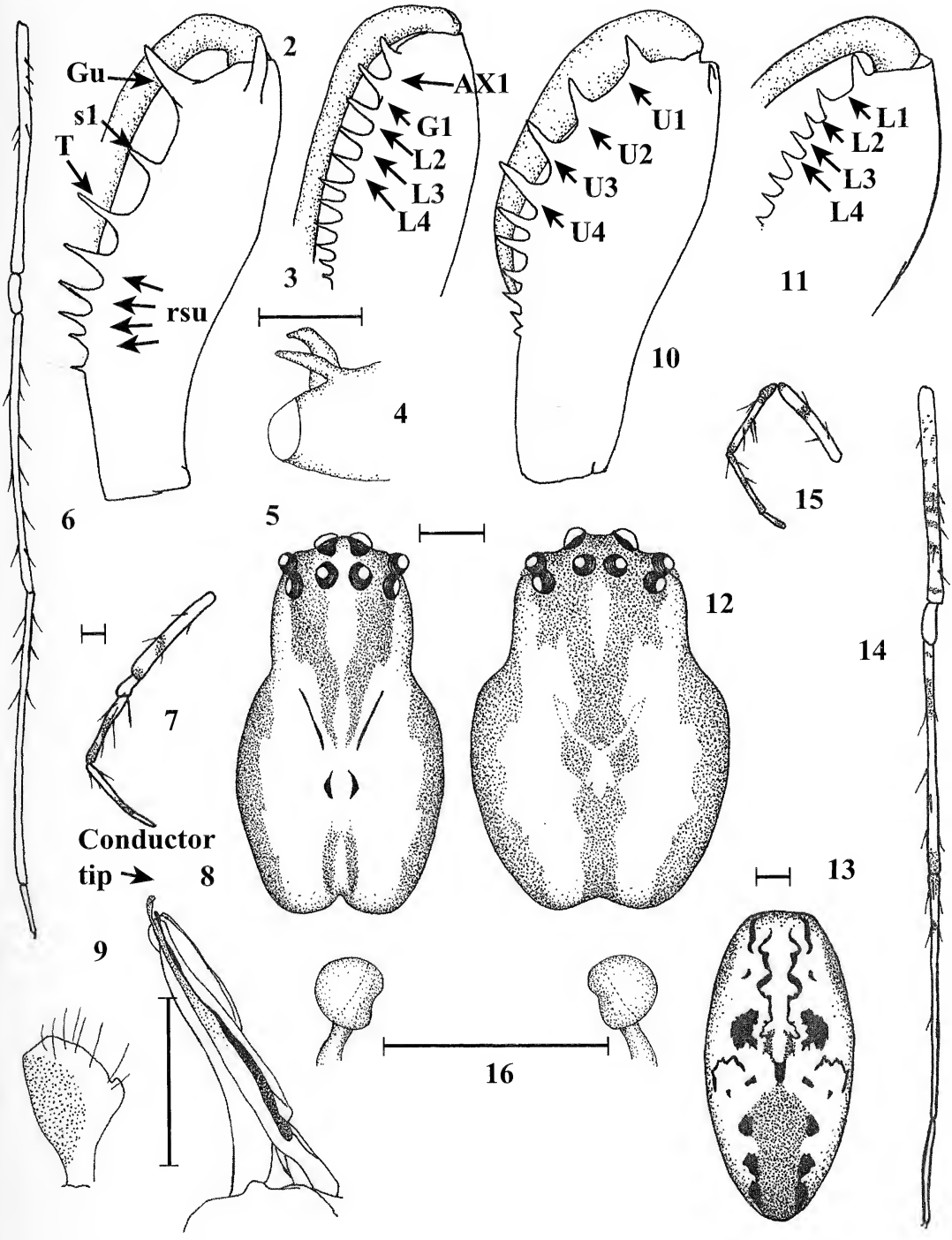
METHODS

Characters examined.—Morphological measurements taken were the same as those described in Gillespie (1991, 1992, 1994): eye separation; cheliceral tooth pattern; form and setation of the first and third legs (I and III representing the greatest divergence in leg function); and form and pattern of the dorsum and carapace. In order to estimate variability within a taxon and determine which features best characterize a species, where possible measurements were taken on six individuals of each sex of each species with additional observations on other individuals once diagnostic characters had been identified. Genitalia of both sexes were examined using the methods described in Gillespie (1991).

Terminology.—The terminology for the teeth on the cheliceral margins of the males is that used in previous papers (Gillespie 1991; Okuma 1987, see Figs. 2, 3, 8, 10, 11). Setation on femora, tibiae and metatarsi of legs I & II is denoted by: fI, fIII, tI, tIII, mI and mIII. CITR refers to the cheliceral inter-tooth ratio, the ratio of 3 lengths: (1) between distal end of male chelicerae to sl; (2) s1 to T; and (3) T to rsu1. The majority of the specimens were collected by myself (RGG) and George Roderick (GKR). The holotype of *T. oomea* has been deposited in the MNHN; all others have been deposited in the BPBM. All paratypes will be deposited in the Essig Museum of Entomology of the University of California, Berkeley EMUC. Unless indicated otherwise, all measurements are in mm.

DISCUSSION

Four new species of *Tetragnatha* endemic to the Marquesas Islands, *T. punua*, *T. oomua*, *T. kapua*, and *T. tahuata*, are described, expanding the total number of endemic species on the islands from one (*T. marquesiana*) to



Figures 2–16.—*Tetragnatha marquesiana* Berland: Male holotype. 2. Promargin of right chelicera; 3. Retromargin of left chelicera; 4. Dorsal spur of right chelicera, lateral; 5. Carapace, dorsal; 6. Right leg I, dorsal; 7. Right leg III, prolateral; 8. Distal end of left palpus, ventral; 9. Left paracymbium, lateral. Female allotype. 10. Promargin of right chelicera; 11. Retromargin of left chelicera; 12. Carapace, dorsal; 13. Abdomen, dorsal; 14. Right leg I, dorsal; 15. Right leg III, prolateral; 16. Seminal receptacles, ventral. Scale bars = 0.5; that between Figs. 2 & 3 applies to Figs. 2, 3, 4, 10, & 11; that between Figs. 5 & 12 applies to Figs. 5 & 12; that between Figs. 6 & 7 applies to Figs. Fig. 6, 7, 14 & 15; that between Figs. 8 & 9 applies to Figs. 8 & 9.

five. On the oldest island, Nuku Hiva, two species (*T. marquesiana* and *T. punua*) and perhaps three (*T. oomua*) occur in sympatry, suggesting that there has been some adaptive radiation, with divergence of ecological roles. However, the divergence is not nearly as pronounced as in the Hawaiian Islands (Gillespie et al. 1997). *Tetragnatha nitens* is the only non-endemic species of *Tetragnatha* in the islands. The finding of this cosmopolitan species at high elevations in the islands might suggest that the species is indigenous (Berland 1933). However, given that the sites from which the species was collected, despite their elevation, were all very disturbed, it could be that *T. nitens* is not indigenous, but rather a more recent introduction to the islands. The Marquesas were once home to a large population of Polynesians, and although the native population suffered a catastrophic demise in the years following European contact, mostly through disease, the landscape had already been extensively modified. Currently, even at high elevations, there are large areas of pasture and tree plantations (e.g. a large portion of the Toovii Plateau and Terre Déserte), and it is only from these areas that *T. nitens* has been collected.

KEY TO SPECIES

1. Lateral eyes well separated (Figs. 20, 27, 45, 52) 2
   Lateral eyes contiguous or almost so (Figs. 5, 12, 36, 60, 67) 7
2. Males 3
   Females 5
3. Dorsal spur of chelicerae and first two marginal teeth (s1 and T) all large and clustered near apex of chelicerae (Levi 1981: 299, fig. 31; Okuma 1987: 84, fig. 31a) ..... *T. nitens*
   Dorsal spur of chelicerae and first two marginal teeth not clustered (Figs. 2, 17, 33, 42, 58) 4
4. Gu very large (largest tooth on promargin of chelicerae) and broad (Fig. 42); embolus pointed at tip (Figs. 48, 74) ..... *T. kapua*
   Gu small, nearly the smallest tooth on promargin of chelicerae (Fig. 17); embolus bifurcated into cup-shaped receptacle at tip (Fig. 73) ..... *T. punua*
5. Prominent tooth at apex of underside of chelicerae pointing straight up, parallel to the cheliceral margin (Levi 1981: 299, fig. 25; Okuma 1987: 84, fig. 31 h) ..... *T. nitens*
   No prominent tooth at apex of underside of chelicerae (Figs. 11, 26, 51, 66) 6
6. First 2 teeth on promargin of chelicera much smaller than next 2 teeth (Fig. 50); spermathecae small and almost spherical (Fig. 56) ..... *T. kapua*
   First 2 teeth on promargin of chelicera similar in size to next 2 teeth (Fig. 25); spermathecae oval-seed shaped (Fig. 32) ..... *T. punua*
7. Males 8
   Females 10
8. Gu very large (largest tooth on promargin of chelicerae) and tall (Fig. 2); conductor and embolus almost straight along length (Fig. 8), tips rounded (Fig. 72) ..... *T. marquesiana*
   Gu absent, or small relative to other teeth on promargin of chelicerae (Figs. 33, 57). Conductor and embolus angular along length, tip pointed or bifurcated (Figs. 40, 63, 75) 9
9. Gu absent (Fig. 33); conductor blunt and slightly bifurcated (Fig. 40) ..... *T. oomua*
   Gu present, small, situated between sl and dorsal spur (Fig. 57); conductor angular, pointed at tip (Figs. 63, 75) ..... *T. tahuata*
10. Spermathecae single spherical / heart-shaped bulb (Fig. 16) ..... *T. marquesiana*
    Spermathecae two bulbs, larger anterior bulb connected to smaller posterior bulb (Fig. 71) ..... *T. tahuata*

Tetragnatha marquesiana Berland (Figs. 2–16, 72)

Tetragnatha marquesiana Berland 1935b: 58, figs. 42–46; Roewer 1942: 986; Bonnet 1959: 4339.

Types.—Holotype male from Marquesas Islands: *Ua Pou:* Vaihakaatiki, Hakahetau, 1000 m, approximately 9.40°S, 140.08°W, November 1931, G. LeBronnec (BPBM), examined.

Other material examined.—Marquesas Islands: *Ua Huka:* Mt Hitikau, 970 m, 8.92° S, 139.55° W, R. Englund, 2 November 1999, 1 ♂, 1 ♀, 5 immatures (EMUC); *Nuku Hiva:* Mt Tekao, 1185 m, 8.86°S, 140.17°W, RGG, June 2000, 4 ♂, 10 ♀, 49 immatures (EMUC); 1100 m, RGG, June 2000, 1 ♂, 1 ♀, 4 immatures (EMUC); 1200 m, RGG, June 2000, 2 ♀, 3 immatures (EMUC); Toovii, Old Road, 1100 m, 8.86°S, 140.18°W, RGG, June 2000, 1 ♀, 1 immature (EMUC).

Diagnosis.—*Tetragnatha marquesiana* is most similar to *T. kapua* on Hiva Oa. It differs in the closer proximity of the lateral eyes (compare Figs. 5 & 6 to Figs. 45 & 52), the much stronger dorsal tooth on the male chelicerae (compare Figs. 2 & 42) and the relative positions of the conductor and embolus tips (compare Figs. 72 & 74).

Redescription.—*Holotype male* (Figs. 2–9, 72)*:* Length of carapace 2.8, total length 6.5. Chelicerae 73% length of carapace. Cheliceral fang slightly shorter than base, bent over at both proximal and distal ends. Promargin of chelicerae (Fig. 2): Gu very long, bent up and out; distance between apex, Gu, s1, and T approximately equal, CITR approximately 0.3: 0.4:0.3; s1 tall spike, longer than wide (somewhat more than half width and height of T); T quite large, though much smaller than Gu, pointing slightly up and out from margin of chelicerae; rsu 6 large, straight spikes, decreasing in size proximally. Retromargin of chelicerae (Fig. 3): total of 11 teeth; AX1 large, prominent; G1 similar in size, pointing slightly up and out, L2–L10 showing slight decrease in size proximally. Dorsal spur fairly long and almost straight (16% length of carapace); tip pointed (Fig. 4). Thoracic fovea distinctly marked around depression (Fig. 5). Coloration and eye pattern as in female. Leg setation similar to female (Figs. 6–7). Conductor (Figs. 8, 72) almost entirely straight, bent over at tip; embolus straight, tip minutely club-like below conductor. Paracymbium shaped like mitten with prominent "thumb" (Fig. 9).

Allotype female (Figs. 10–16)*:* Length of carapace 2.7, total length 7.1. Chelicerae 74% length of carapace. Cheliceral fang slightly greater than half length of base, tapering to smooth point distally. Promargin of chelicerae (Fig. 10): 10 teeth, U1 stout, pointing straight up, slightly wider, shorter than U2 and quite well separated (17% cheliceral length) from U2; U2 quite long, U3 longer, U4 longest; U5–U10 decreasing in size proximally. Retromargin of chelicerae (Fig. 11): series of 8 teeth: L1 similar in size to U1, larger than L2. Remaining retromarginal teeth similar in height, decreasing slightly in width proximally. Posterior eyes slightly wider than distance between them. Median ocular area slightly narrower posteriorly (Fig. 12); lateral eyes contiguous. Carapace brown with very pronounced markings including dark margins. Abdomen elongate oval; dorsum dark orange-brown with quite elaborate folium and paired markings down sides (Fig. 13). Legs heavily banded (Figs. 14–15). Leg spines medium length and robust; setation: fI 2/3/4; tI 3/2/3; mI 2/1/2; fIII 2 dorsal, 1 ventral; tIII 2 dorsal, 1 lateral, 2 ventral; and mIII 1 dorsal and 1 ventral macrosetae. Seminal receptacles (Fig. 16): single spherical or heart-shaped sphere.

Variation (*n* = 4 ♂, 4 ♀).—Male: Cephalothorax 2.6–2.8. CITR little variation; rsu 6–7. Female: Length of carapace 2.6–2.8. Color patterns vary quite considerably, from yellow/gold through mostly maroon-dark red to dark greenish and brown; no polymorphism.

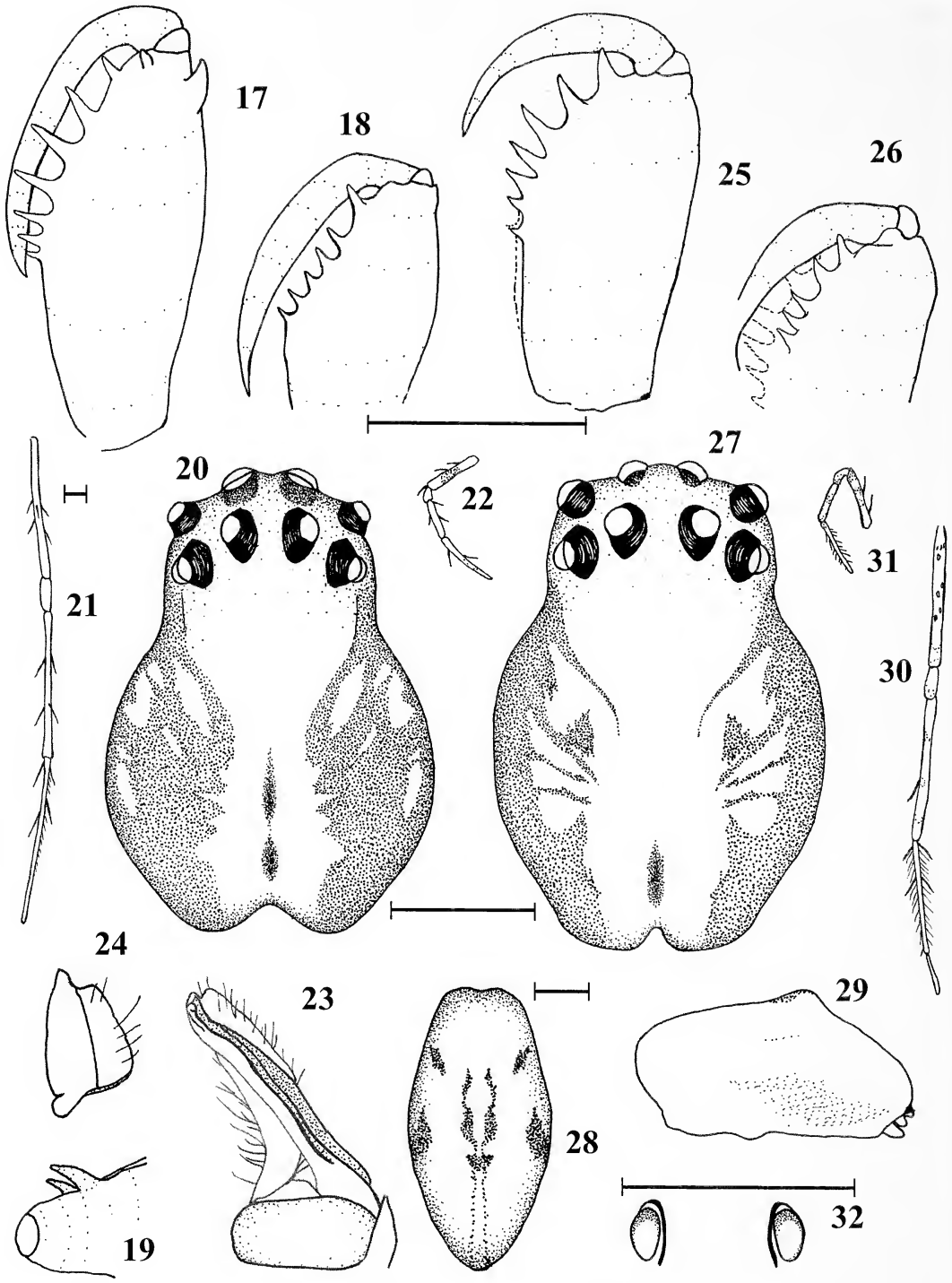
Natural history.—The type specimen of *T. marquesiana* was collected from *Freycinetia* on the island of Ua Pou (Berland 1935b). This species appears to predominate in high elevation montane forest on Nuku Hiva, Ua Huka, and Ua Pou, and can be quite abundant, building webs mostly low down in the mossy crevices of trees in the wet forest.

Tetragnatha punua new species
(Figs. 17–32, 73)

Types.—Holotype male from Marquesas Islands: *Nuku Hiva:* Mt Tekao, 1185 m, 8.86°S, 140.17°W, June 2000, RGG (BPBM). Paratypes: Marquesas Islands: *Nuku Hiva:* 3 males, 2 females, 1 immature, Mt Tekao, 1185 m, 8.86°S, 140.17°W, June 2000, RGG (EMUC).

Etymology.—The specific epithet, a noun in apposition, is the Marquesan word for a small animal, and refers to the diminutive size of this species.

Diagnosis.—*Tetragnatha punua* is separated from other species by the bifurcated tip of the conductor (Figs. 23, 73) and cheliceral dentition (Figs. 17, 18) in the male, and by the shape of the seminal receptacles (Fig. 32)



Figures 17–32.—*Tetragnatha punua*: Male holotype. 17. Promargin of right chelicera; 18. Retromargin of left chelicera; 19. Dorsal spur of right chelicera, lateral; 20. Carapace, dorsal; 21. Right leg I, dorsal; 22. Right leg III, prolateral; 23. Left palpus, ventral; 24. Left paracymbium, lateral. Female allotype. 25. Promargin of right chelicera; 26. Retromargin of left chelicera; 27. Carapace, dorsal; 28. Abdomen, dorsal; 29. Abdomen, lateral; 30. Right leg I, dorsal; 31. Right leg III, prolateral; 32. Seminal receptacles, ventral. Scale bars = 0.5; that between Figs. 18 & 25 applies to Figs. 17, 18, 19, 25, 26; between Figs. 20 & 27 applies to Figs. 20 & 27; at Fig. 21 applies to Figs. 21, 22, 30, & 31; at 28 applies to Figs. 28 & 29; at Fig. 32 applies to Figs. 23, 24 & 32.

and cheliceral dentition (Figs. 25, 26) in the female.

Description.—*Holotype male* (Figs. 17–24, 73)*:* Length of carapace 1.6, total length 3.8. Chelicerae short, 57% length of carapace. Cheliceral fang a good deal shorter than base, curved over at both proximal and distal ends. Promargin of chelicerae (Fig. 17): Gu represented by prominent tooth dorsal/lateral to sl (between sl and dorsal spur); distance between apex, Gu, sl, and T approximately equal, CITR approx. 0.3:0.4:0.3; sl small point, longer than wide (just over half width and height of T); T relatively small, pointing slightly up and out from margin of chelicerae; rsu 5 large, straight spikes, decreasing in size. Retromargin of chelicerae (Fig. 18): total of 6 teeth; AX1 absent; G1 prominent, pointing slightly up and out, L2–L5 similar in size. Dorsal spur very short and squat (11% length of carapace); tip pointed (Fig. 19). Thoracic fovea indistinct (Fig. 20). Coloration and eye pattern as in female. Leg setation similar to female (Figs. 21–22). Conductor (Figs. 23, 73) almost straight, tip bifurcated into cup-shape. Paracymbium with unequal lobes (Fig. 24).

Allotype female (Figs. 25–32)*:* Length of carapace 1.6, total length 4.2. Chelicerae 46% length of carapace. Cheliceral fang slightly greater than half length of base, tapering to smooth point distally. Promargin of chelicerae (Fig. 25): 7 teeth, U1 large, stout, bending upwards, wider and slightly longer than U2 and fairly well separated (13% cheliceral length) from U2; U2 very slightly shorter than U1 and U3, U3–U7 decreasing slightly in size proximally. Retromargin of chelicerae (Fig. 26): series of 5 teeth: L1 smaller than U1, similar in size to L2. Remaining retromarginal teeth smaller, similar in size to each other. Posterior eyes wide, much wider than distance between them. Median ocular area almost square (Fig. 27); lateral eyes slightly separated. Carapace brown with very pronounced, broad, dark markings along margins. Abdomen elongate oval, slightly dilated at midline (Fig. 28) and with a single hump when viewed from side (Fig. 29); dorsum brown with a few paired markings down sides and along midline. Legs well banded and spotted (Figs. 30–31). Leg spines sparse, medium length; setation: fI 0/0/0; tI 2/0/0; mI 2/0/2; fIII with 2 dorsal only, and tIII and mIII without macrosetae. Seminal receptacles (Fig. 32): single bulb, shaped like sprouting bean seed.

Variation (*n* = 3 ♂, 2 ♀).—Male: Cephalothorax 1.4–1.6. CITR little variation; rsu sometimes 6. Female: Length of carapace 1.5–1.6. Color patterns vary slightly; no polymorphism.

Natural history.—*Tetragnatha punua* has not, to my knowledge, been collected before. It is found in the high montane wet forest of Mt. Tekao. The spider is relatively uncommon, and was not immediately distinguished in the field from immature *T. marquesiana* with which it co-occurs. Accordingly, I am not yet clear as to what ecological differences exist between this species and *T. marquesiana*.

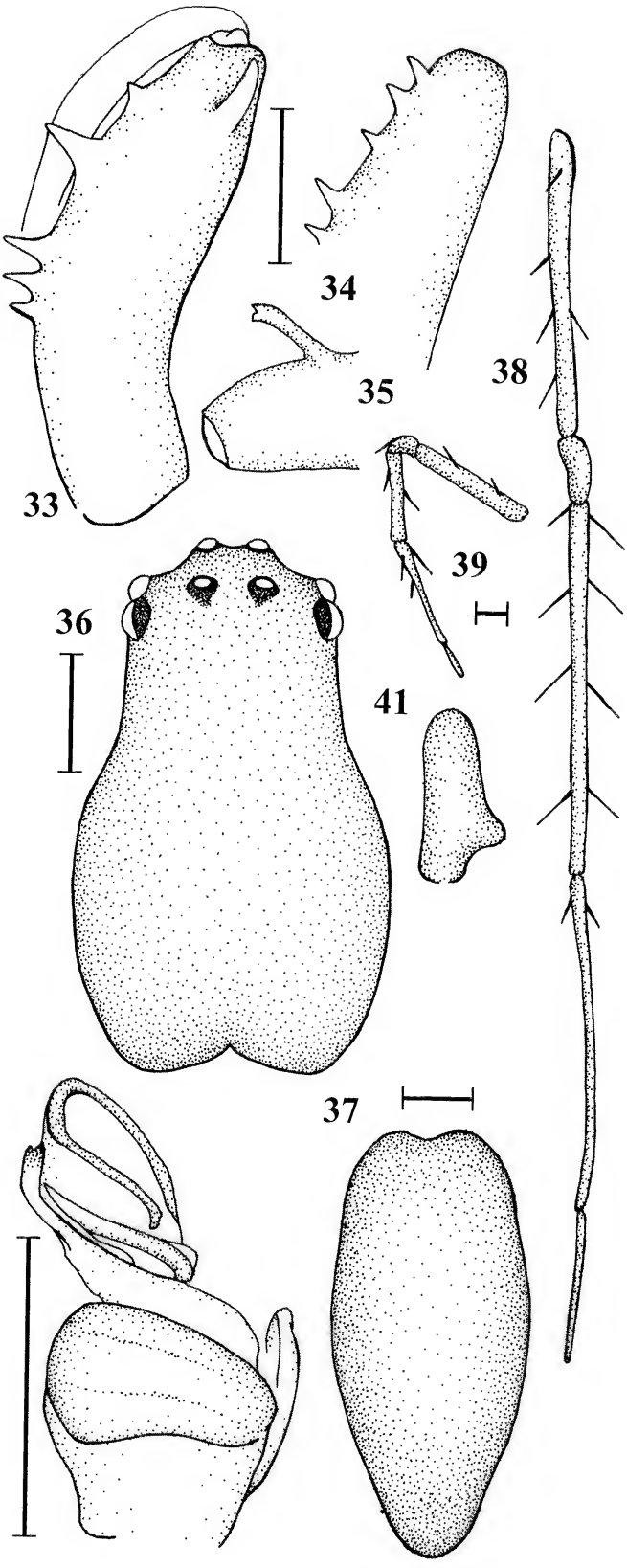
Tetragnatha oomua new species
(Figs. 33–37)

Type.—Holotype male from Marquesas Island: *Nuku Hiva:* Oomua, approximately 8.8°S, 140.2°W, 1931, G. LeBronnec (MNHN).

Etymology.—The specific epithet, a noun in apposition, refers to Oomua, the mountain in the central range of mountains in Nuku Hiva which is the type locality of this species.

Diagnosis.—*Tetragnatha oomua* is very distinct from all other species of *Tetragnatha* based on the shape of the conductor tip (Fig. 40) and the cheliceral armature (Figs. 33, 34).

Description.—*Holotype male* (Figs. 33–41)*:* Length of carapace 2.2, total length 5.2. Chelicerae 71% length of carapace. Cheliceral fang slightly shorter than base, bent over at both proximal and distal ends. Promargin of chelicerae (Fig. 33): Gu absent; distance between apex, sl, and T approximately equal, CITR approx. 0.3:0.3:0.4; sl small point, as long as wide (approximately 30% width and height of T); T tall, straight point, much larger than all other teeth; rsu 3 straight spikes, decreasing in size proximally. Retromargin of chelicerae (Fig. 34): total of 5 teeth; AX1 absent; G1 quite small, L2, L4–L5 similar in size; L3 smaller than other teeth. Dorsal spur long, curved over (18% length of carapace); tip slightly bifurcated (Fig. 35). Posterior eyes small, substantially smaller than distance between them. Median ocular area slightly wider posteriorly (Fig. 36); lateral eyes contiguous. Coloration and markings indistinct, although the specimen was quite old, and colors may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have faded. Abdomen elongate oval (Fig. 37). Legs unmarked but with long macrosetae (Figs. 38–39): fI 3/1/2; tI 3/1/3; mI 1/0/1; fIII with 2 dorsal only, tIII with 1 dorsal, 1 lateral, and mIII with 2 dorsal, 1 lateral macrosetae. Conductor (Fig. 40) thick and bent, bifurcated at tip. Paracymbium with blunt lateral projection from near base (Fig. 41).

Remarks.—There is a single specimen of this spider, which was labeled *T. macilenta* by Berland. However, *T. macilenta* has not yet been found in the Marquesas. *Tetragnatha oomua* is a very distinctive animal, quite different from *T. macilenta* L. Koch (compare fig. 16, p. 63 in Okuma 1987).

Tetragnatha kapua new species
(Figs. 42–56, 74)

Types.—Holotype male from Marquesas Island: *Hiva Oa:* Temetiu ridge, 1170m, 1185m, 9.81°S, 139.08°W, RGG and GKR, June 2000 (BPBM). Paratypes: Marquesas Island: *Hiva Oa:* 1 ♂, 2 immatures, Kaava, 930 m, January 1932, G. LeBronnec (BPBM); 2 ♂, 2 ♀, 12 immatures, Temetiu ridge, 1170 m, 9.81°S, 139.08°W, June 2000, RGG; 1 ♂, 1 ♀, 4 immatures, same data except 26 October 1999, R. Englund (EMUC); 4 immatures, Ootua, 875 m, 9.77°S, 138.97°W, June 2000, RGG (EMUC).

Etymology.—The specific epithet, a noun in apposition, is the Marquesan word for mountain- or ridge-top and refers to the habitat where this species occurs.

Diagnosis.—*Tetragnatha kapua* is most similar to *T. marquesiana* from the northern islands of the archipelago. It differs in having the lateral eyes farther apart (Figs. 45, 52), whereas they are contiguous in *T. marquesiana*. It can also be distinguished by the smaller dorsal tooth (Fig. 42) compared to *T. marquesiana* (Fig. 2) and by the relative positions of the conductor and embolus (compare Figs. 48 & 74 to Figs. 8 & 72).

Description.—*Holotype male* (Figs. 42–49, 74)*:* Length of carapace 2.3, total length 4.4. Chelicerae 68% length of carapace. Cheliceral fang slightly shorter than base, bent over at both proximal and distal ends. Promargin of chelicerae (Fig. 42): Gu very large and broad; distance between apex, Gu, s1, and T approximately equal, CITR approximately 0.3:0.3:0.4; s1 small point, longer than wide (approximately half width and height of T); T small relative to remaining teeth and Gu pointing slightly up and out from margin of chelicerae; rsu 6 large, straight spikes, decreasing in size proximally. Retromargin of chelicerae (Fig. 43): total of 6 teeth; AX1 large, prominent; G1 quite small and pointing straight out, L2–L5 showing slight increase in size proximally. Dorsal spur not long, curved over (11% length of carapace); tip pointed (Fig. 44). Thoracic fovea distinctly marked around depression (Fig. 45). Coloration and eye pattern as in female. Leg setation similar to female (Figs. 46 & 47). Conductor (Figs. 48, 74) almost entirely straight, except for a slight "wiggle" near tip, and pointed. Paracymbium with unequal lobes (Fig. 49).

Allotype female (Figs. 50–56)*:* Length of carapace 2.2, total length 5.2. Chelicerae 64% length of carapace. Cheliceral fang slightly greater than half length of base, tapering to smooth point distally. Promargin of chelicerae (Fig. 50): 8 teeth, U1 short, pointing straight up, similar width, shorter than U2 fairly well separated (13% cheliceral length) from U2; U2 fairly large, bent up, U3 taller than other teeth; U4–U7 decreasing slightly in size proximally. Retromargin of chelicerae (Fig. 51): series of 7 teeth: L1 considerably larger than U1, similar in size to L2. Remaining retromarginal teeth decreasing slightly in length and width proximally. Posterior eyes slightly wider than distance between them. Median ocular area almost square (Fig. 52); lateral eyes well separated. Carapace brown with very pronounced markings including dark margins. Abdomen elongate oval; dorsum brown with paired markings down sides (Fig. 53). Legs well marked with bands and spots (Figs. 54

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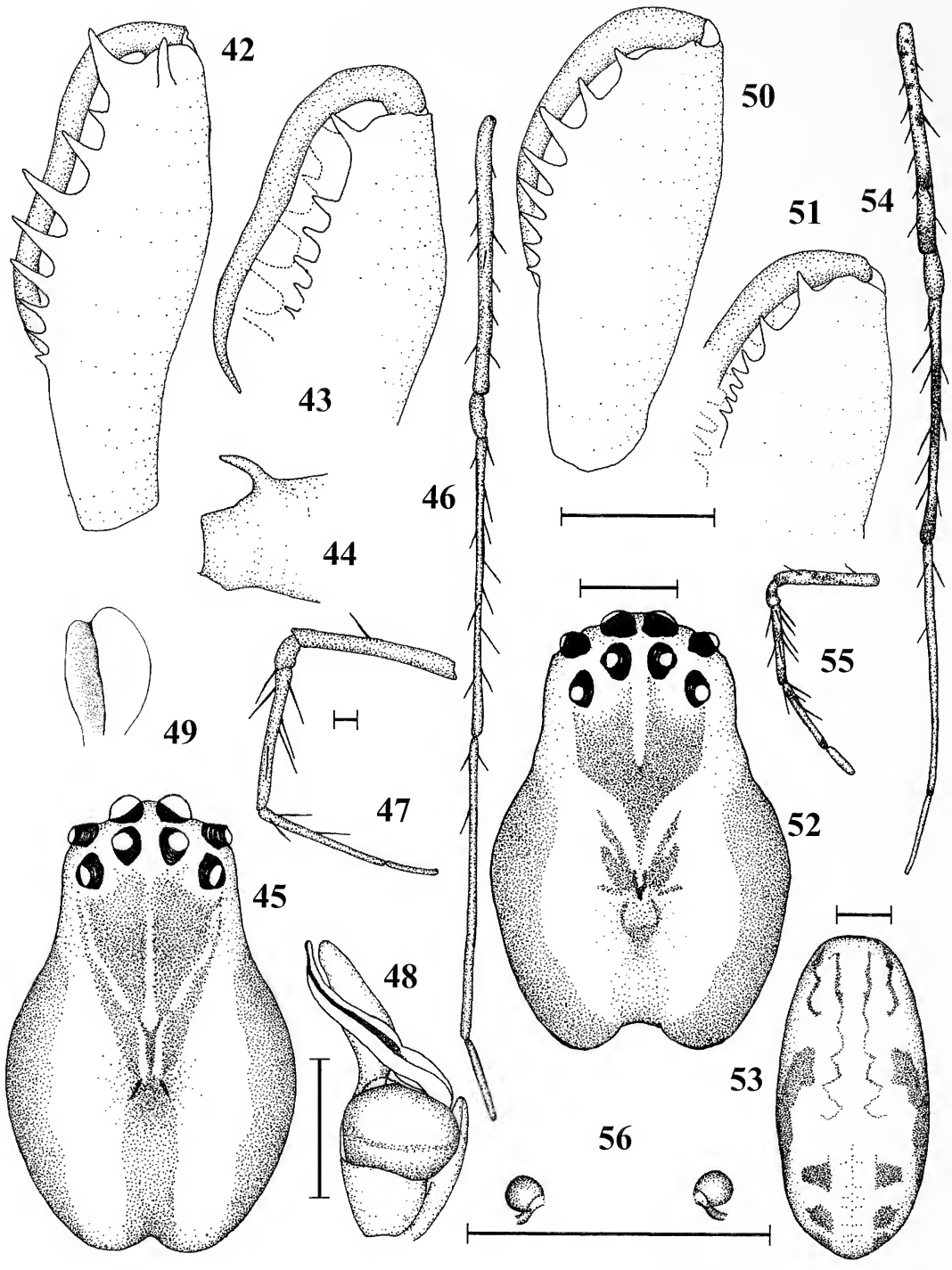
Figures 33–41.—*Tetragnatha oomua*: Male holotype. 33. Promargin of right chelicera; 34. Retromargin of left chelicera; 35. Dorsal spur of right chelicera, lateral; 36. Carapace, dorsal; 37. Abdomen, dorsal; 38. Right leg I, dorsal; 39. Right leg III, prolateral; 40. Left palpus, ventral; 41. Left paracymbium, lateral. Scale bar = 0.5; that between Figs. 33 & 34 applies to Figs. 33, 34, & 35; that between Figs. 38 & 39 applies to Figs. 38 & 39; that at Fig. 40 applies to Figs. 40 & 41.



Figures 42–56.—*Tetragnatha kapua*: Male holotype. 42. Promargin of right chelicera; 43. Retromargin of left chelicera; 44. Dorsal spur of right chelicera, lateral; 45. Carapace, dorsal; 46. Right leg I, dorsal; 47. Right leg III, prolateral; 48. Left palpus, ventral; 49. Left paracymbium, lateral. Female allotype. 50. Promargin of right chelicera; 51. Retromargin of left chelicera; 52. Carapace, dorsal; 53. Abdomen, dorsal; 54. Right leg I, dorsal; 55. Right leg III, prolateral; 56. Seminal receptacles, ventral. Scale bar = 0.5; that between Figs. 50 & 51 applies to Figs. 42, 43, 44, 50, & 51; at Fig. 52 applies to Figs. 45 & 52; at 47 applies to Figs. 46, 47, 54, & 55; at Fig. 48 applies to Figs. 48 & 49.

& 55). Leg spines medium length and robust; setation: fI 6/2/4; tI 3/1/3; mI 1/1/1; fIII with 2 dorsal only, tIII with 2 dorsal, 2 lateral, and 2 ventral, and mIII with 1 dorsal, 2 lateral and 2 ventral macrosetae. Seminal receptacles (Fig. 56): simple, single, small bulb.

Variation (*n* = 3 ♂, 2 ♀).—Little variation among those specimens examined. Color patterns vary slightly; no polymorphism.

Natural history.—*Tetragnatha kapua* is the predominant species on Hiva Oa. It builds webs in low vegetation on the mountain ridge cloud forests of Hiva Oa.

Remarks.—A male specimen of this species was initially described as a co-type of *T. marquesiana*. Berland (1935b) stated (in translation): "In this specimen, one notes a certain difference from the type: the two subapical teeth of the chelicerae are shorter, and the internal is thicker, the tibia of the palp is shorter than the tarsus." Berland went on to place two female specimens from Hiva Oa in *T. marquesiana* with the comment that (in translation): "I think I can assign two females from Hiva Oa to this species, characterized by a short abdomen, swollen in the middle; I do not give the drawing of their chelicerae, because I am not sure these specimens are adult."

Tetragnatha tahuata new species
(Figs. 57–71, 75)

Types.—Holotype male from Marquesas Island: *Tahuata:* Haaopi summit, 900 m, approximately 9.93°S, 139.10°W, July 1930, G. LeBronnec (BPBM).

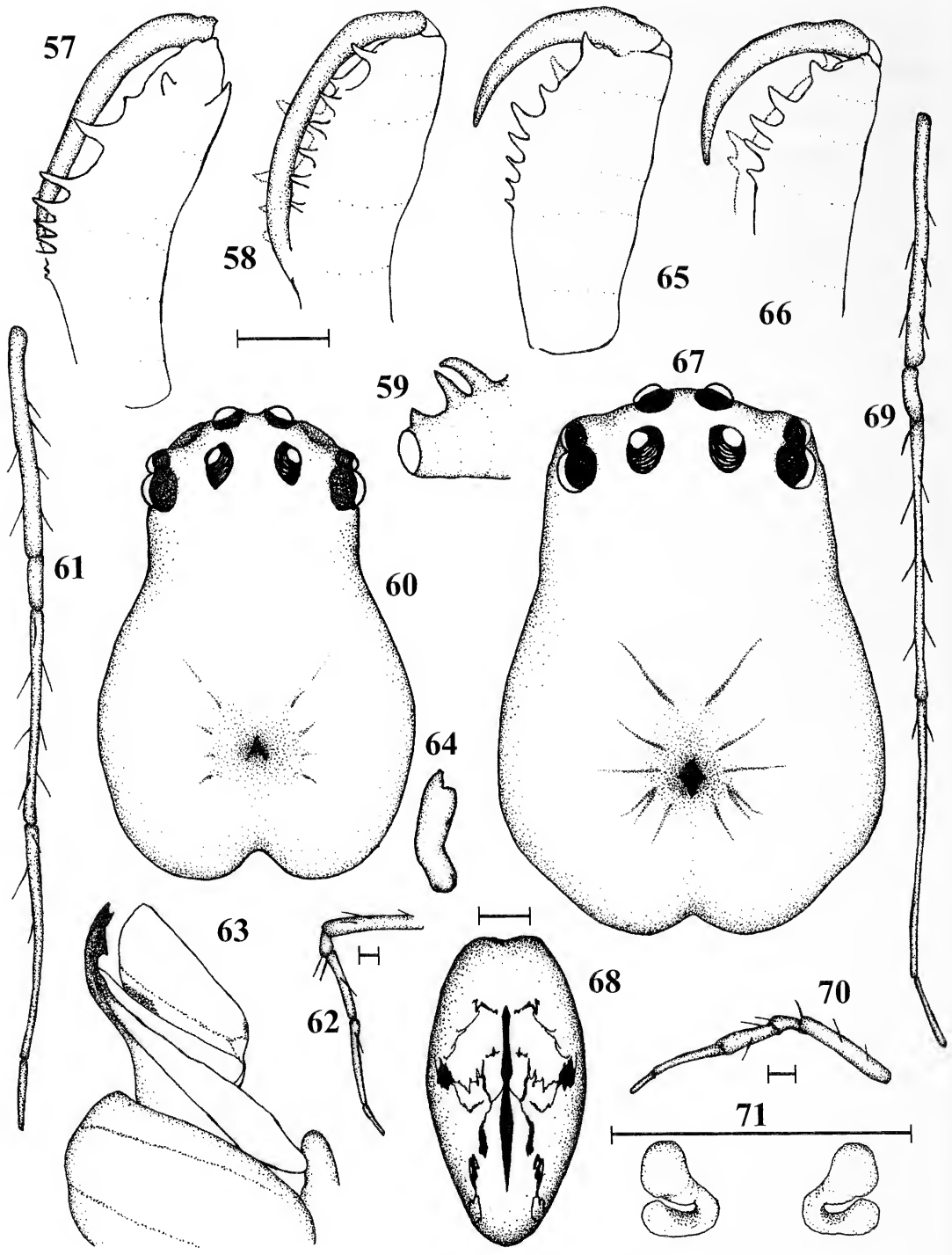
Etymology.—The specific epithet, a noun in apposition, refers to Tahuata, the name of the island in which this species occurs, and the type locality of the species.

Diagnosis.—*Tetragnatha tahuata* is distinct from all other species of *Tetragnatha* based on the shape of the conductor tip (Figs. 63, 75) and the cheliceral armature (Figs. 57, 58) of the male, and the seminal receptacles of the female (Fig. 71).

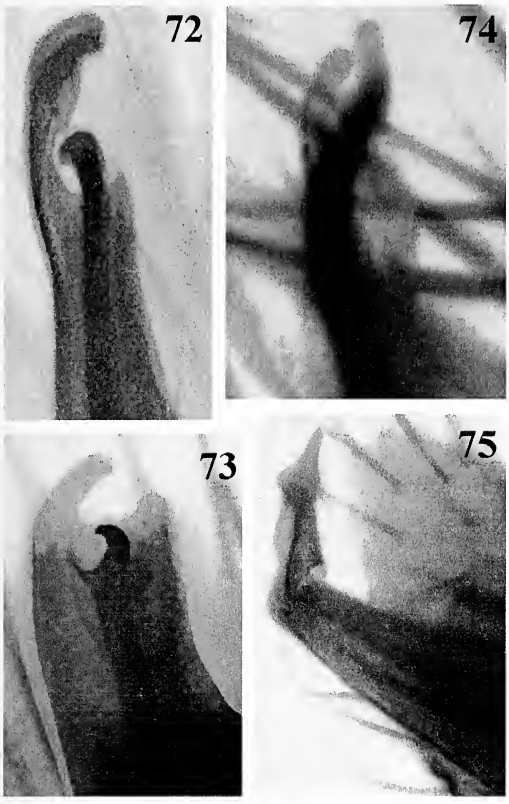
Description.—*Holotype male* (Figs. 57–64, 75): Length of carapace 2.5, total length 4.8. Chelicerae 81% length of carapace. Cheliceral fang slightly shorter than base, bent over at both proximal and distal ends. Promargin of chelicerae (Fig. 57): Gu represented by large and prominent tooth dorsal/lateral to sl (between sl and dorsal spur); distance between apex and s1 much less than between s1 and T, CITR approx. 0.5:0.2:0.3; s1 very small point (approximately 20% width and height of T); T large, pointing slightly up and out from margin of chelicerae; rsu 7 straight spikes, decreasing in size proximally. Retromargin of chelicerae (Fig. 58): total of 6 teeth; AX1 large, prominent; G1 slightly smaller and pointing straight out, L2–L5 showing slight decrease in size proximally. Dorsal spur quite long, curved up and over (14% length of carapace); tip blunt (Fig. 59). Thoracic fovea indistinct (Fig. 60). Coloration and eye pattern as in female. Leg setation similar to female (Figs. 61, 62). Conductor (Fig. 63, 75) angular below tip, tip pointed; embolus thin and curved round. Paracymbium narrow, bent, uneven at apex (Fig. 64).

Allotype female (Figs. 65–71): Length of carapace 2.9, total length 6.0. Chelicerae 57% length of carapace. Cheliceral fang slightly greater than half length of base, tapering to smooth point distally. Promargin of chelicerae (Fig. 65): 7 teeth, U1 prominent, pointing up and out, larger than U2 and very well separated (20% cheliceral length) from U2; U2 short, U3 taller than other teeth; U4–U7 decreasing in size proximally. Retromargin of chelicerae (Fig. 66): series of 5 teeth: L1 slightly smaller than U1, much smaller than L2. Remaining retromarginal teeth decreasing slightly in length and width proximally. Posterior eyes slightly wider than distance between them. Median ocular area slightly wider posteriorly (Fig. 67); lateral eyes contiguous. Carapace brown with indistinct markings. Abdomen elongate oval, slightly dilated at midline; dorsum light brown with fairly irregular markings down sides (Fig. 68). Legs unmarked (Figs. 69–70). Leg spines fairly short; setation: fI 2/0/4; tI 3/1/3; mI 2/1/0; fIII with 2 dorsal only, tIII with 1 dorsal, 1 lateral, and mIII without macrosetae. Seminal receptacles (Fig. 71): larger anterior bulb connected to smaller posterior bulb.

Remarks.—The specimens described here are the only known representatives of the species. They were labeled *T. macilenta* by Berland (1933), who commented that the specimens he was looking at were (in translation): "Very similar. . . to those [specimens of *T. macilenta*] described by L Koch from Samoa and Tonga, in particular in the chelicerae of the male and the female, also in the shape of



Figures 57–71.—*Tetragnatha tahuata*: Male holotype. 57. Promargin of right chelicera; 58. Retromargin of left chelicera; 59. Dorsal spur of right chelicera, lateral; 60. Carapace, dorsal; 61. Right leg I, dorsal; 62. Right leg III, prolateral; 63. Left palpus, ventral; 64. Left paracymbium, lateral. Female allotype. 65. Promargin of right chelicera; 66. Retromargin of left chelicera; 67. Carapace, dorsal; 68. Abdomen, dorsal; 69. Right leg I, dorsal; 70. Right leg III, prolateral; 71. Seminal receptacles, ventral. Scale bar = 0.5; that between Figs. 57 & 58 applies to Figs. 57, 58, 59, 65, 66; at Fig. 62 applies to Figs. 61 & 62; at Fig. 70 applies to Figs. 69 & 70; at Fig. 68 applies to Fig. 68; at Fig. 71 applies to Figs. 63, 64, & 71.



Figures 72–75.—High magnification photographs of conductor of male palps: 72. Tetragnatha *marquesiana*; 73. *T. punua*; 74. *T. kapua*; 75. *T. tahuata*.

the female abdomen, unevenly rounded; there are however some small differences in the cheliceral dentition . . . . likewise in the eyes, the anterior lateral ones being smaller than the posterior laterals, which does not seem to agree with the description of L Koch." As the description above indicates, the specimen bears little resemblance to *T. macilenta* as described by Koch (1872, p. 192, T. XVI, fig. 6 and T. XVII, fig. 1; see also Okuma 1987, fig. 16, p. 63).

Tetragnatha nitens (Audouin)

Eugnatha nitens Audouin in Savigny 1826: 118, pl. 2, fig. 2.
Eugnatha pelusia Audouin in Savigny 1826: 119, pl. 2, fig. 3.
Tetragnatha andina Taczanowski 1878: 144, pl. 1, fig. 2.
Tetragnatha antillana Simon 1897: 868; Seeley 1928: 104, figs. 1–4; Roewer 1942: 988; Chickering 1957: 306, figs. 1–6; Bonnet 1959: 4318; Chickering 1962: 428, figs. 1–6.
Tetragnatha vicina Simon 1897: 869.
Tetragnatha peninsulana Banks 1898: 246, pl. 15, fig. 12.
Tetragnatha galapagoensis Banks 1902: 61, pl. 1, fig. 10.
Tetragnatha aptans Chamberlin 1920: 41, figs. 7–8.
Tetragnatha eremita Chamberlin 1924: 645, figs. 89, 90.
Tetragnatha seminola Gertsch 1936: 10, figs. 22, 23.
Tetragnatha steckleri Gertsch & Ivie 1936: 19, figs. 31–33.
Tetragnatha elmora Chamberlin & Ivie 1942: 62, fig. 160.
Tetragnatha festina Bryant 1945: 407, figs. 38, 39, 41.
Tetragnatha haitensis Bryant 1945: 408, fig. 37.
Tetragnatha nitens (Audouin in Savigny): Roewer 1942: 978; Bonnet 1959: 4345; Okuma 1968: 40, figs. 9–16; Levi 1981: 291, pl. 5a-b, figs. 23–34; Okuma 1983: 75; Okuma 1987: 84, fig. 31.

Material examined.—In the Marquesas Islands, *T. nitens* has been collected from the following localities (material in BPBM): *Eiao:* 1 ♂, 5♀, Vaituha Valley, 300 m, 8.00°S, 140.68°W, October 1929, found in grass on edge of little lake, A. Adamson; *Nuku Hiva:* 1♂, 6♀, Vaihakameama 1000 m, November 1929, A. Adamson; 1 ♀, same data, except 850 m, June 1931, G. LeBronnec and Tauraa; 1♀, Tapuaooa, 850 m, May 1931, G. LeBronnec and Tauraa; 2♀, Terre Deserte, Ha'atuatua, 850 m, approximately 8.83° S, 140.21° W, July 1988, S. Montgomery; 1♀, 1 immature, Toovii Plateau, 1100 m, approximately 8.87°S, 140.15° W, June 1984, G. Nishida (most specimens determined by Berland 1935a; I examined and confirmed determinations).

Remarks.—*Tetragnatha nitens* was considered indigenous to the Marquesas by Berland (1933). He pointed out that (in translation): "the species is widespread throughout the Mediterranean area (including southernmost France), almost all of Africa to the Cape, Australia, New Zealand, and the Chatham islands; this is the first documentation of the species in Polynesia. Its broad distribution cannot be interpreted as an accidental transport, more especially in the case of the Marquesas because it was found in the interior of two islands and not on the coast as is in general the case for the species fortuitously introduced." Although Berland's argument is sound, it may not hold for habitats that have

been severely impacted through human activity, as have the sites from which *T. nitens* has been collected (see discussion above).

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HABITAT AFFINITIES OF SPIDERS LIVING NEAR A FRESHWATER POND

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ABSTRACT. Habitat ranges of ground-dwelling spiders were studied by pitfall trapping in and around a freshwater pond during the spring and summer of 1998 in central Alberta, Canada. Sixty species from 14 families were collected, and catches of several species suggested distinct habitat affinities along transects between the pond and adjacent terrestrial habitats. Variation in the catches of *Pirata piraticus* (Clerck 1757), *Pardosa moesta* Banks 1892, *Pardosa fuscula* (Thorell 1875), and immature *Pirata* species were partially explained by soil moisture at trap locations extending from the shore. We devised a "floating" pitfall trap that captured several species, including mature and immature *Dolomedes triton* (Walckenaer 1837), *Pirata piraticus*, and other immature Lycosidae, directly on the water surface. A DCA ordination revealed distinct spider assemblages were associated with three habitat types: 1) the water surface; 2) the moist habitats closely associated with the water's edge; and 3) the drier, terrestrial grassland habitats located >2 m from the shore. A new, more inclusive definition of semi-aquatic spiders was developed, based on knowledge about both male and female activity near the shore, and affinities towards soil moisture. Thus, *Pirata piraticus*, *Dolomedes triton*, and *Pardosa fuscula* were defined as semi-aquatic spiders.

Keywords: Habitat gradient, soil moisture, semi-aquatic, floating pitfall trap

Many spiders are associated with freshwater ecosystems. For example, the diversity and general ecology of spiders inhabiting peatlands in Canada, Denmark and Germany have been examined (Nørgaard 1951; Dondale & Redner 1994; Schikora 1994), as has the spider fauna of rice fields (e.g., Heiss & Meisch 1985; Oraze & Grigarick 1989). Much work has also focused on the biology and habitat affinities of nursery web spiders (Pisauridae), especially those in the genus *Dolomedes* Latreille 1804 (e.g., Bleckmann & Lotz 1987; Zimmermann & Spence 1989, 1998; Jordan et al. 1994). Few detailed studies of spider assemblages living near freshwater habitats such as small ponds exist, however, so little is known about the diversity, abundance, and habitat selection of semi-aquatic spiders outside of bogs and rice fields.

Aquatic organisms derive respiratory oxygen entirely from the surrounding water environment (Miall 1895). The term "semi-aquatic" has been used to refer to organisms that spend part of their lives in or on water, but which generally obtain oxygen from the air (Ward 1992). Under this definition, *Dolomedes triton* (Walckenaer 1837), found at the margins of ponds, is accurately described as semi-aquatic. This spider is capable of moving rapidly over the surface film (Suter & Gruenwald 2000), and does so in response to vibrations of potential insect prey (Shultz 1987). Also, insects such as whirligig beetles (Coleoptera, Gyrinidae) and water striders (Hemiptera, Gerridae), which also forage on the surfaces of freshwater ponds, are considered semi-aquatic (Spence 1986; Merritt & Cummins 1996). However, many species not usually considered to be aquatic or semi-aquatic live and forage in the upper littoral zone of a freshwater body, perhaps because of a moisture preference or requirement.

Spiders in various families occur around bodies of water. Some spiders, in particular wolf spiders (Lycosidae), are commonly collected in ombrotrophic bogs (Nørgaard 1951; Itamies & Jarva-Karenlampi 1989), so one might expect to find them in or near a freshwater pond. Spiders in the family Linyphiidae have long been known to have affinities with moisture (Huhta 1965), and many build small webs on damp ground near the surface of wa-

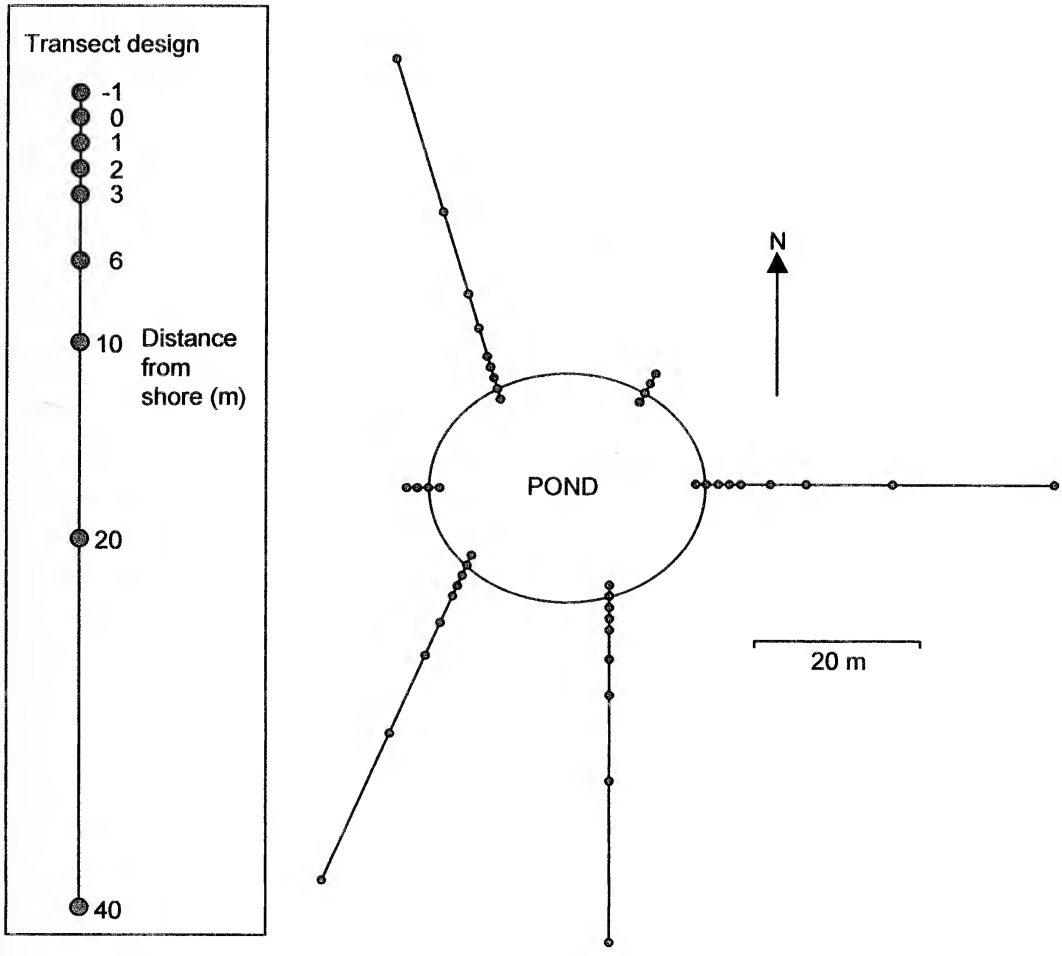

Figure 1.—Sampling design, depicting series of pitfall traps (circles, 6 floating, 38 terrestrial) along transects extending from a freshwater pond.

ter (Kaston 1981). Pisaurids and hahniids are also commonly observed near freshwater (Carico 1973; Opell & Beatty 1976; Suter 1999).

In this study we used pitfall traps to collect gound-dwelling spiders along a habitat gradient starting with the pond surface and extending into the adjacent terrestrial system. We sought to determine: 1) which ground-dwelling species have affinities to the aquatic habitat; 2) the relationship between species abundance and soil moisture; and 3) which species have the potential to forage on the water surface.

METHODS

Study sites and sampling design.—This research was conducted at the George Lake Field Site (53°57′N, 114°06′W), located approximately 85 km NW of Edmonton, Alberta, Canada. Habitats in and around "Meadow Pond" were chosen for study. This permanent freshwater pond, measuring about 22 by 29 m, was constructed in 1970 in a small meadow cleared from continuous upland *Populus* forest the previous year. The pond was surrounded immediately by mixed grasses and short shrubs, and a forest dominated by *Populus* trees was located 30–40 m from the pond's edge [see Niemelä et al. (1992) for detailed description].

Pitfall traps were placed in six transects around the pond (Fig. 1). Four transects consisted of nine traps, the first placed in the pond 1 m from shore ("floating" trap, see description below), and the rest embedded in the ground and extending to a distance of 40 m from the pond as illustrated in Fig. 1. Two

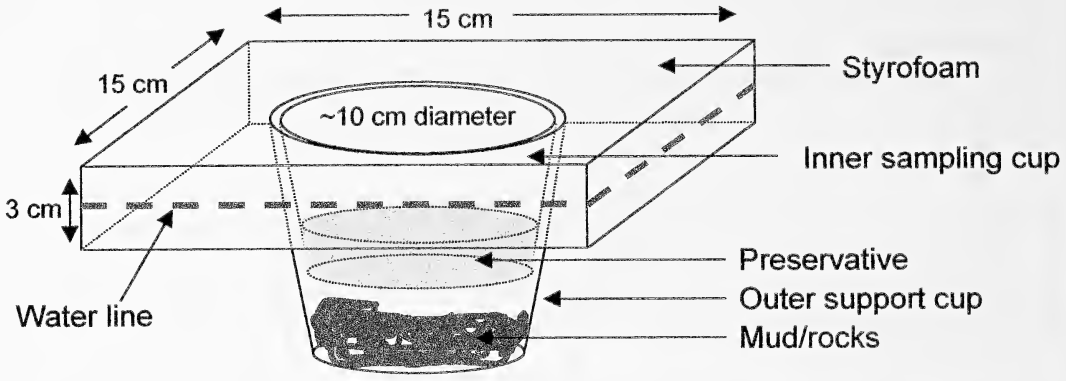

Figure 2.—Design of floating pitfall trap. Styrofoam platform was secured to desired location by an anchoring pole, and covered by a 15 by 15 cm plywood roof (not shown).

shorter transects contained only four traps, the first a floating trap and the others at 0, 1 and 2 m from shore (Fig. 1). Short transects were used specifically to amplify data about spiders living near the shore. Traps were open from 21 May–06 September 1998 and emptied every 10–15 days.

Each terrestrial pitfall trap consisted of a 1 L plastic sleeve container buried so its lip was level with the ground surface. A close-fitting sampling cup containing 2–3 cm of silicate-free ethylene glycol was placed inside each plastic sleeve, and traps were covered with supported plywood roofs (15 by 15 cm) to minimize disturbance and rainwater dilution of the preservative [see Spence & Niemelä (1994) for additional details].

We constructed a novel "floating" pitfall trap to catch skating spiders or those ballooning onto open water. These traps were similar to standard terrestrial pitfall traps, but the plastic containers and sampling cups were held afloat in a one inch thick piece of Styrofoam™ (15 by 15 cm), and weighed down with mud and rocks so that they sat at the water surface (Fig. 2). Each trap was tied to an anchoring pole, and was fitted with a plywood roof measuring 15 by 15 cm.

Soil samples were taken with a circular metal soil corer (15 cm diameter) along each transect at 0, 2, 6 and 20 m from the shore to obtain gravimetric estimates of percent soil moisture along the habitat gradient. Soil samples were taken in early July to coincide with the general peak in spider activity around Meadow Pond. Also, we took the samples five days after a heavy rainfall to ensure that the soil was not over-saturated in certain locations. All samples were weighed, allowed to dry for a week at 40°C and then reweighed.

Spider identifications.—Individual spiders were sorted and identified using various taxonomic keys (e.g., Dondale & Redner 1978, 1982, 1990; Kaston 1981; Platnick & Dondale 1992) and reference collections at the Strickland Entomological Museum (University of Alberta, Edmonton, Alberta, Canada). If necessary, species identifications were verified by D.J. Buckle. Since species identifications are based primarily on genitalia, only sexually mature spiders were identified to species—juveniles were identified to genus whenever possible. Voucher specimens are deposited in the Strickland Entomological Museum.

Data analyses.—Pitfall trap captures depend on movement of individuals and therefore estimate activity and density of species, as well as their susceptibility to trapping (Topping & Sunderland 1992). Since pitfall traps measure this "activity-density," it is difficult to truly detect both absolute abundance and male to female ratios (e.g. Topping &Sunderland 1992; Spence & Niemelä 1994). Even with these limitations, however, pitfall traps are still among the most commonly used sampling technique for collecting spiders, and can offer significant insights into the biology, ecology, life-history and habitat affinities of spiders (e.g., Uetz & Unzicker 1976; Pajunen et al. 1995; Buddle 2000; Buddle et al. 2000). Capture data from the pond transects were analyzed graphically to portray general trends in relative abundance of common species (defined as those comprising >1% of the total catch), separated by gender, as a function of distance from the shore. Since trapping effort

varied with distance from shore (i.e., short transects increased sampling effort near shore), data were presented as the number collected per trap.

Linear regression was used to test if soil moisture was related to trap distance from the shore, and to determine whether the catches of common species and numbers of immatures were dependent upon the gradient in relative soil moisture. Data lacking homogeneity of variance were transformed [$x' = \ln(x+1)$] prior to regression analyses.

Data were also interpreted by detrended correspondence analysis (DCA), an ecological ordination technique useful in revealing variations among data and identifying critical factors associated with species distribution patterns (Jongman et al. 1995). Ordination analyses were done using the program PC-ORD (McCune & Mefford 1999); all species were included in the analysis but rare species were downweighted in proportion to their frequency. Rare species were defined as those represented by fewer than F/5 individuals, where F represents the frequency of the most common species collected (McCune & Mefford 1999). Immature specimens were excluded prior to analysis.

RESULTS

Spider species and habitat ranges.—In total, 3145 individuals representing a rich spider assemblage that included 60 species in 14 families were collected by pitfall trapping across the transects (Table 1). Nine common species (i.e., represented by >50 individuals, or >1% of the total collection) composed about 72% of the total catch, and *Pardosa moesta* Banks 1892 alone made up about one third of spiders collected (Table 1). Immature specimens in the genera *Pardosa*, *Pirata*, and *Trochosa* accounted for about 13% of the total collection (Table 1). About 52% of the sexually mature individuals collected were males, and this sex ratio remained similar regardless of of trap location (Table 1).

Several of the more common species were collected at or near the pond shore. *Dolomedes triton* (mature and immature specimens) was trapped most often in floating traps (Table 1), while the relative abundance of *Pirata piraticus* (Clerck 1757) and *Pardosa fuscula* (Thorell 1875) were greatest at the pond shore for both males and females (Figs. 3A, B). Immature *Pirata* were also most frequently collected close to shore (Fig. 3C). Male and female *Neoantistea magna* (Keyserling 1887) were common near the shoreline (Figs. 3D, E), but were also occasionally collected in terrestrial traps located further from the shore (Figs. 3D, E, Table 1). *Pardosa moesta* was more uniformly distributed across the terrestrial traps, although its capture rates were clearly higher between 2 and 10 m from shore (Figs. 3A, B). Patterns with the other common wolf spiders (Lycosidae) were less clear: *Trochosa terricola* Thorell 1856 did not show any affinities towards the pond shore, and immature *Trochosa* were most common about 2–10 m from shore (Figs. 3A, B, C). Collections of immature *Pardosa* were highly variable (Fig. 3C) and thus difficult to assign to any particular region of the habitat gradient. The three most common linyphiids, *Allomengea dentisetis* (Grube 1861), *Bathyphantes pallidus* (Banks 1892) and *Grammonota gigas* (Banks 1896) were generally active in the middle or toward the land-based ends of transects and were rarely collected directly adjacent to the pond shore (Figs. 3D, E). Females of these species were relatively uncommon in our samples (Figs. 3D, E, Table 1).

Although sample sizes were smaller, some of the more rarely collected species (i.e., <50 individuals) also showed affinities towards the shore. For example, immature *Dolomedes*, immature *Neoantistea*, and the linyphiid *Erigone atra* Blackwall 1833 were all most commonly collected <3 m from shore (Table 1). A total of eight taxa were collected in traps floating on the water surface (Table 1). Of these, *Dolomedes triton* (mature and immature), *Pirata piraticus*, and immature *Pirata* were most commonly collected.

Catch rates and soil moisture.—Soil moisture decreased significantly with increasing distance from the shore (linear regression, $Y = 21.29 - 0.58X$, $df = 18$, $R^2 = 0.25$, $P = 0.028$). Collections of four spider taxa showed significant relationships with relative soil moisture (Fig. 4). Captures of *P. fuscula* and *Pirata piraticus* adults and immature *Pirata* spp. were positively associated with soil moisture (Figs. 4B, C, D). Activity of *P. moesta* showed an opposite trend, increasing as soil moisture decreased (Fig. 4A). The remaining common taxa showed no relationship with our measures of soil moisture.

Table 1.—Summary of spider species collected by floating and terrestrial pitfall traps in or near a freshwater pond. Data provided as MALE/FEMALE, and (IMMATURE) specimens, and totals across all traps. * indicate the most commonly collected taxa.

Family, species	Floating traps	Traps <3 m from shore	Traps 3 to 40 m from shore	Male/ Female Total	TOTAL
Amaurobiidae					
Cybaeopsis euopla (Bishop & Crosby 1935)		0/1	2/10	2/11	13
Immature		(2)	(4)	—	6
Araneidae					
Araniella displicata (Hentz 1847)			0/1	0/1	1
Larinioides cornutus (Clerck 1757)		0/1		0/1	1
Clubionidae					
Clubiona kulczynskii Lessert 1905			1/0	1/0	1
Immature		(1)	(7)	—	8
Gnaphosidae					
Drassyllus niger (Banks 1896)		1/0	1/1	2/1	3
Gnaphosa borea Kulczynski 1908		1/0		1/0	1
Gnaphosa parvula Banks 1896		2/9	4/4	6/13	19
Haplodrassus hiemalis (Emerton 1909)		0/1	4/1	4/2	6
Micaria pulicaria (Sundevall 1832)		1/2	2/2	3/4	7
Zelotes fratis Chamberlin 1920		5/6	15/5	20/11	31
Immature		(10)	(20)	—	30
Hahniidae					
Neoantistea magna (Keyserling 1887)*		78/75	41/8	119/83	202
Neoantistea (immature)		(9)	(3)	—	12
Linyphiidae					
Allomengea dentisetis (Grube 1861)*		11/0	40/7	51/7	58
Aphileta misera (O.P.-Cambridge 1882)			0/1	0/1	1
Bathyphantes pallidus (Banks 1892)*		5/3	31/12	36/15	51
Centromerus sylvaticus (Blackwall 1841)		0/4	0/6	0/10	10
Ceratinella brunnea Emerton 1882			0/1	0/1	1
Ceratinopsis stativa (Simon 1881)		1/0		1/0	1
Diplocentria bidentata (Emerton 1882)		1/0	1/1	2/1	3
Eperigone trilobata (Emerton 1882)			1/0	1/0	1
Erigone atra Blackwall 1833	1/0	8/3	1/2	10/5	15
Gonatium crassipalpum Bryant 1933			1/1	1/1	2
Grammonota gigas (Banks 1896)*		36/11	49/12	85/23	108
Hybauchenidium cymbadentatum (Crosby & Bishop 1935)			0/1	0/1	1
Meioneta sp. A			0/1	0/1	1
Microlinyphia pusilla (Sundevall 1829)		0/4	2/1	2/5	7
Microneta viaria (Blackwall 1841)		0/1	2/1	2/2	4
Neriene radiata (Walckenaer 1841)			0/1	0/1	1
Pityohyphantes costatus (Hentz 1850)			0/1	0/1	1
Pocadicnemis americana Millidge 1975		1/0		1/0	1
Scotinotylus exsectoides Millidge 1981		0/1		0/1	1
Walckenaeria atrotibialis (O.P.-Cambridge 1878)		0/1	2/0	2/1	3
Walckenaeria communis (Emerton 1882)		0/18	0/16	0/34	34
Walckenaeria fusciceps Millidge 1983		1/0		1/0	1
Walckenaeria spiralis (Emerton 1882)		1/0		1/0	1
Zornella cultrigera (L. Koch 1879)			1/0	1/0	1
Immature		(1)	(1)	—	2

Table 1.—Continued.

Family, species	Floating traps	Traps <3 m from shore	Traps 3 to 40 m from shore	Male/ Female Total	TOTAL
Liocranidae					
Agroeca ornata Banks 1892		2/1	1/3	3/4	7
Agroeca pratensis Emerton 1890		3/2	2/9	5/11	16
Scotinella pugnata (Emerton 1890)		1/0		1/0	1
Lycosidae					
Alopecosa aculeata (Clerck 1757)		7/4	6/6	13/10	23
Arctosa emertoni Gertsch 1934		3/4	2/2	5/6	11
Pardosa distincta (Blackwall 1846)			3/0	3/0	3
Pardosa fuscula (Thorell 1875)*		82/65	1/6	83/71	154
Pardosa mackenziana (Keyserling 1877)			0/5	0/5	5
Pardosa moesta Banks 1892*	0/1	147/234	293/421	440/656	1096
Pardosa xerampelina (Keyserling 1877)		6/9	6/8	12/17	29
Pirata insularis Emerton 1885		4/0	1/0	5/0	5
Pirata piraticus (Clerck 1757)*	69/67	242/55	5/5	316/127	443
Trochosa terricola Thorell 1856*		9/43	11/35	20/78	98
Alopecosa (immature)		(1)	(5)	—	6
Arctosa (immatre)		(2)		—	2
Pardosa (immature)*	(4)	(90)	(69)	—	163
Pirata (immature)*	(19)	(72)	(4)	—	95
Trochosa terricola (immature)*	(1)	(58)	(87)	—	146
Mimetidae					
Ero caionis Chamberlin & Ivie 1935			1/0	1/0	1
Pisauridae					
Dolomedes triton (Walckenaer 1837)*	34/21	2/0		36/21	57
Dolomedes (immature)	(20)	(2)		—	22
Salticidae					
Immature		(1)		—	1
Tetragnathidae					
Pachygnatha clercki Sundevall 1830		1/0		1/0	1
Pachygnatha tristriata C.L. Koch 1845			1/1	1/1	2
Pachygnatha sp. A		0/3		0/3	3
Immature	(1)	(4)	(4)	—	9
Theridiidae					
Euryopsi argentea Emerton 1882		0/1		0/1	1
Thomisidae					
Ozyptila sincera canadensis Dondale & Redner 1975		6/0	20/2	26/2	28
Xysticus britcheri Gertsch 1934		1/1	1/1	2/2	4
Xysticus elegans Keyserling 1880		0/1		0/1	1
Xysticus ellipticus Turnbull, Dondale & Redner 1965		4/5	10/0	14/5	19
Xysticus emertoni Keyserling 1880		5/1	16/2	21/3	24
Xysticus ferox (Hentz 1847)		2/0	3/0	5/0	5
Immature		(2)	(12)	—	14
TOTAL	104/89 (45)	680/570 (255)	584/603 (215)	1368/1262	3145

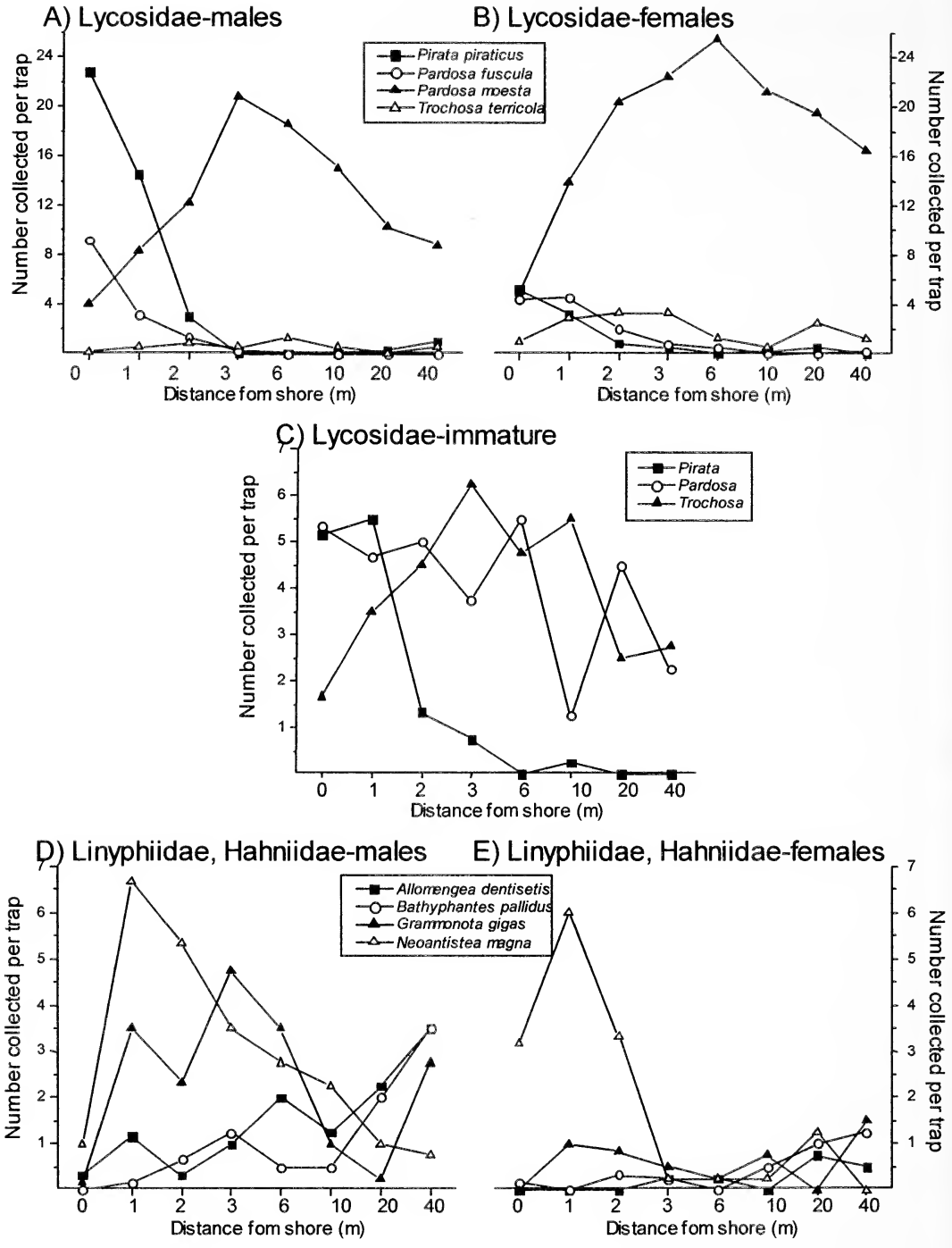

Figure 3.—Number of male, female and immature spiders collected per pitfall trap for common species in the families Lycosidae (A, B, C), Linyphiidae and Hahniidae (D, E) sampled along transects extending from the shore of pond. These taxa account for 84.4% of the total number of individuals collected in all but floating traps.

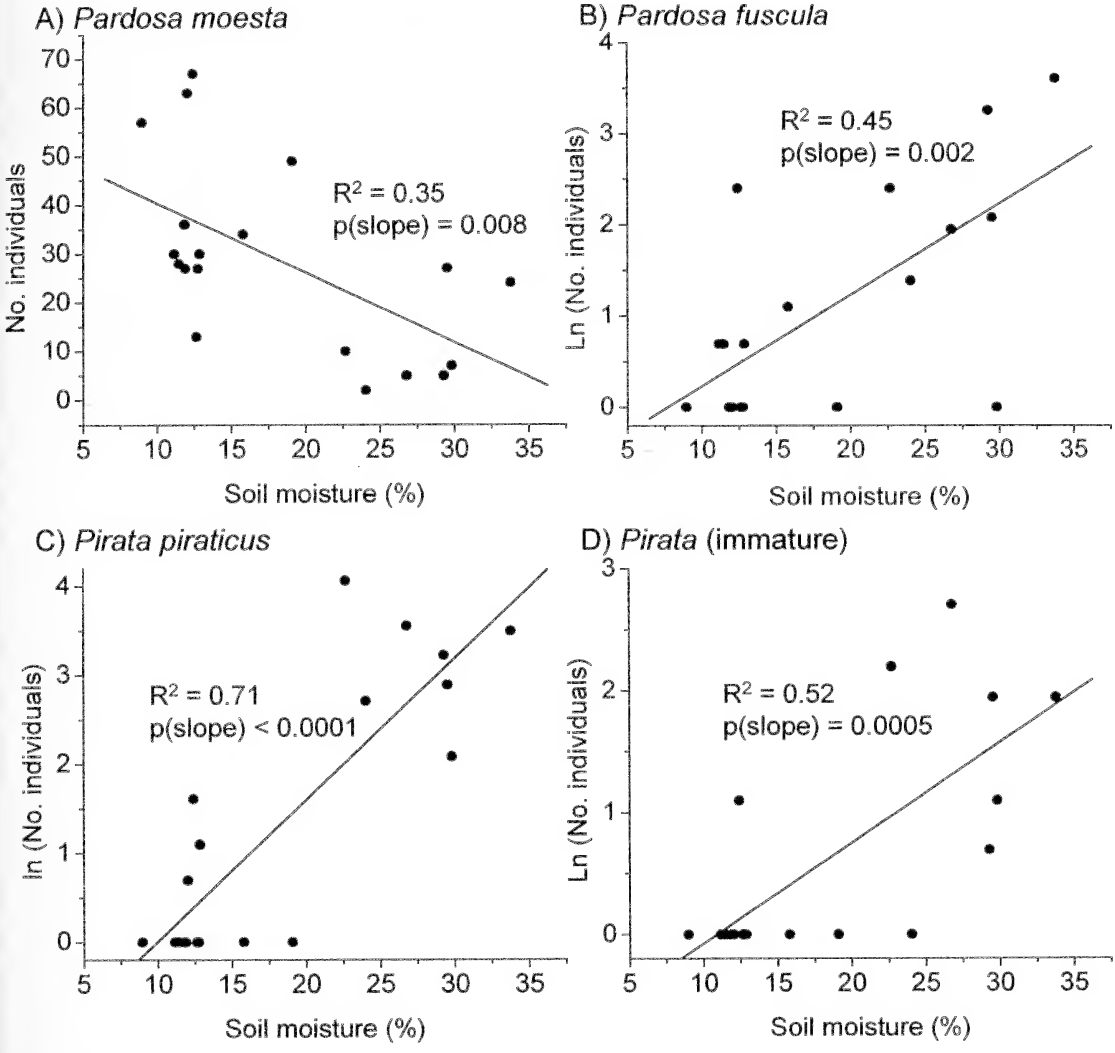

Figure 4.—Linear regression of catches of *Pardosa moesta*, *P. fuscula*, *Pirata piraticus*, and immature *Pirata* against soil moisture (%). All but data for *P. moesta* ln-transformed prior to analyses (note scale on y-axis).

Community patterns.—DCA analysis of data from the 38 terrestrial and 6 floating pitfall traps, and 60 spider species, yielded a high eigenvalue of 0.629 for Axis 1, suggesting that a single environmental variable explains most of the variation in the ordination (Fig. 5). The positions of various traps along the first DCA axis closely reflect their similarity in terms of species composition. Floating traps, which caught the same few species and most *D. triton* (Table 1), grouped together, and shore traps (at shore, 1 m and 2 m from shore) occupied similar positions along Axis 1 (Fig. 5). In particular, species scores for *D. triton*, *Pirata piraticus*, *Pardosa fuscula*, and *Neoantistea magna* were closest to floating traps and the terrestrial pitfall traps close to shore (Fig. 5). Traps at >2 m from the shore had lower scores along Axis 1 and contained more variation along Axis 2. The positions of two traps with high sample scores along Axis 2 are associated with high catches of *A. dentisetis* and *B. pallidus*, as reflected by their species scores (Fig. 5). Species scores for *T. terricola*, *Grammonota gigas*, and *Pardosa moesta* were located more centrally in the ordination space, which reflects their relative ubiquity along sampling transects (Fig. 5).

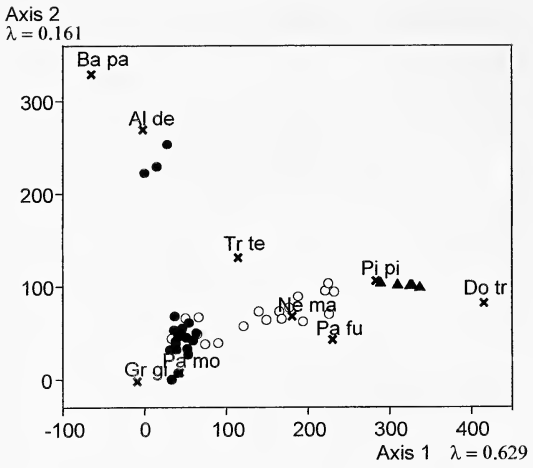

Figure 5.—Sample scores (pitfall traps) and selected species scores from DCA ordination (Axes 1 and 2) derived from 44 samples and 60 spider species. λ indicates eigenvalues for axes 1 and 2. Triangles are floating traps, open circles are terrestrial pitfall traps located at 0, 1, and 2 m from shore, and solid circles are pitfall traps > 2 m from shore. Species scores (**x**) depicted for the 9 most commonly collected species: *Allomengea dentisetis* (Al de), *Bathyphantes pallidus* (Ba pa), *Dolomedes triton* (Do tr), *Grammonota gigas* (Gr gi), *Neoantistea magna* (Ne ma), *Pardosa fuscula* (Pa fu), *Pardosa moesta* (Pa mo), *Pirata piraticus* (Pi pi), and *Trochosa terricola* (Tr te).

DISCUSSION

Habitat ranges.—Our results indicate that a gradient between a pond and an adjacent forest habitat supports a diverse assemblage of spiders, and several common species had strong associations with one part of the gradient. *Pirata piraticus* and *Pardosa fuscula*, for example, were associated with moist littoral areas, *Pardosa moesta* was more common in open, dry grassy regions, and *D. triton* was most often caught on the pond surface.

Habitat ranges of *D. triton*, and *Pirata piraticus* were most strongly associated with the water surface. Since both males and females of these species showed the same distributions in capture rates, it is likely that reproduction is occurring on, at, or near the pond surface. *Dolomedes* species live near permanent bodies of freshwater, such as small ponds and streams (Carico 1973; Shultz 1987; Zimmermann & Spence 1989, 1998; Suter 1999). Our findings for *D. triton* were similar, as our collections of adults of this species were concentrated on the water rather than near the pond (Table 1, Fig. 5). The lycosid genus *Pirata* Sundevall 1833 may be collected near ponds and lakes, or in bogs, swamps, marshes and deep meadows (Wallace & Exline 1978). In our study, *Pirata* species were most common on the pond surface or on land close to the shore. Clearly, *D. triton* and *Pirata piraticus* are active in and strongly associated with the pond's upper littoral zone.

Pardosa moesta alone accounted for 35% of all spiders collected. Males and females were common between 3–10 m from shore although individuals of both sexes were also collected in traps nearer to or farther from the shore. In contrast, *Pardosa fuscula* (males and females) was most common at or near the pond shore (Figs. 3A & B, 5). Others have noted that *P. fuscula* is associated with moist habitats such as peatlands in eastern Canada (Dondale & Redner 1990, 1994; Koponen 1994).

Trochosa terricola was evenly distributed along the sampling transects. Although Dondale & Redner (1990) suggest this species inhabits shady fields and forest edges, they reported a large number of *T. terricola* in a bog in southern Ontario (Dondale & Redner 1994). Since *T. terricola* was fairly abundant 2 m from shore, and also 20 m from shore, it does not seem to require particular micro-environmental conditions associated with the water's edge.

Distributions observed for the common linyphiids suggest that these spiders were common in a variety of habitats, and that none were strongly associated with the littoral zone community. Ground-dwelling linyphiids typically occupy the leaf-litter matrix in forests (Huhta 1971), and a variety of sources suggest that many species prefer closed-canopy forests (e.g., Pajunen et al. 1995; Buddle et al. 2000). Thus, sampling around a pond located in a closed-canopy forest is predicted to harbor higher catches of linyphiids than were found in our research. Since male and female *E. atra* were collected most frequently near the shore, this species was different from other linyphiids in that it seemed to remain near the pond shore. Although *E. atra* was considered rare in our collection (15 individuals), it is known to build webs adjacent to water, as reported by Kaston (1981); thus, more intensive sampling may show that this species has some

moisture requirement and as such is closely tied to bodies of water.

Catches in the floating traps were distinct from other trap types along Axis 1 in our DCA. Traps >2 m from shore captured spider assemblages that blended into those from shoreline traps as evidenced by the species scores for *T. terricola*, *Grammonota gigas*, and *Pardosa moesta* in the DCA ordination (Fig. 5). In relative terms, these species may be considered generalists with respect to the types of terrestrial habitats tested in this study, and thus are common among terrestrial traps but rare in floating traps. Axis 1 of the DCA ordination explained much of the variation among trap captures, and supports the existence of a simple gradient of spider assemblages based on proximity to the pond: there are distinct spider assemblages (although not without overlap) associated with 1) the water's surface, 2) the habitat directly adjacent to the pond, and 3) the drier grass-dominated meadow located >2 m from the shore.

Without more intensive sampling, it is difficult to assess the habitat affinities of rarely collected species. However, we are able to comment on spiders collected in floating traps, as these had to arrive there via ballooning and/or skating across the water's surface. As such, a total of eight spider taxa have the potential to forage on the water's surface (Table 1), and collectively these spiders may be important predators in semi-aquatic food webs, as has been previously shown with *D. triton* (Zimmermann & Spence 1989.)

Soil moisture.—Few studies have directly examined how a moisture gradient might affect the relative abundance of spider species. Numbers of *Pirata piraticus* increased as soil moisture increased (Fig. 4C), corroborating the idea that this species requires high levels of moisture, higher humidity and lower ground temperature than other wolf spiders (Nørgaard 1951). Palmgren (1972) also suggested that this species is present along shores of freshwater bodies because it has a high light requirement. Therefore, *Pirata piraticus* is most likely adapted to littoral conditions where soil and vegetation are moist and temperatures are cool.

We know of no experiments investigating temperature and moisture requirements of *Pardosa fuscula*. Dondale & Redner (1990, 1994) suggest that this species prefers moist habitats including *Sphagnum* bogs, fens, marshes and meadows. *Pardosa fuscula* was more commonly found near the shore of a freshwater pond than in adjacent terrestrial habitats. Since males and females of this species showed this habitat affinity, it is likely that reproduction occurs close to the water's edge.

Pardosa moesta can be found in meadows, bogs and marshes (Dondale & Redner 1990), and in closed-canopy deciduous forests (Buddle 2000; Buddle et al. 2000). Dondale & Redner (1994) reported much higher numbers of *P. moesta* than either *P. fuscula* or *Pirata piraticus* in wet *Sphagnum* bogs. Although this was also true in our study, 65% of *P. moesta* were captured in the grass habitats >6 m from the pond shore. In addition, captures of this species were negatively associated with soil moisture (Fig. 4A). These results suggest that capture of *P. moesta* in terrestrial habitats is not driven solely by moisture conditions.

Trochosa terricola and the three common linyphiid species were active across much of the habitat gradient but were not significantly associated with our measures of soil moisture. Thus, these species do not have a strong association with soil moisture around our study pond. Opell & Beatty (1976) suggest that *Neoantistea* species build webs on the ground near water to condense moisture and thereby remain active during hot and dry times of the day. Although *N. magna* was common near the water's edge, it is probably not responding directly to moisture and instead may prefer areas where there are suitable depressions on which to anchor small sheet webs.

Semi-aquatic spiders.—We propose a new definition of a semi-aquatic spider as follows: a semi-aquatic spider species is one whose relative abundance is greatest on the water surface or close to the shore (i.e., within 2 m), and which may also have a significant preference or requirement for a moist substrate. Additionally, there must be evidence that these species reproduce on or near the water as inferred by collections of both male and female specimens at these locations. According to these criteria, three spider species from this study may be considered semi-aquatic. *Pirata piraticus* and *Pardosa fuscula* are both active at the pond shore and were strongly associated with moist substrates. *Dolomedes tri-*

ton was collected most often in the water where it walks easily across the surface and fishes for insect prey (Zimmermann & Spence 1989). Although other species in our study were collected more often near the shoreline (e.g., *N. magna*), their occurrence may reflect something other than strict requrirements for moisture. We also believe that more extensive sampling will reveal that some of the more rare species (e.g., *E. atra*) may also fit under our definition for semi-aquatic spiders.

Despite having been the subject of few ecological studies, there are diverse assemblages of spiders living along the gradient between a freshwater pond and its adjacent terrestrial habitats. Our study calls attention to this assemblage and shows that it is an interesting subject for ecological work. Some of these spiders clearly belong to a semi-aquatic or littoral spider community strongly associated with water. Additional studies of these species assemblages, their response to physical factors such as moisture, and role as predators in shoreline communities will provide greater understanding of the importance of semi-aquatic spiders in freshwater ecosystems.

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EGGSAC RECOGNITION IN *LOXOSCELES GAUCHO* (ARANEAE, SICARIIDAE) AND THE EVOLUTION OF MATERNAL CARE IN SPIDERS

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ABSTRACT. We report for the first time the existence of eggsac recognition and maternal care in *Loxosceles gaucho*. Spiders confronted simultaneously with their own and foreign eggsacs stay closer to their own eggsacs. This is unexpected since eggsac recognition should evolve among species with clumped distributions, high maternal investments and few breeding opportunities, features not present in this species. Despite this recognition, spiders with a single eggsac make no distinction between their own and foreign eggsacs: they adopt eggsacs from sympatric, conspecific females, and take care of them as their own. It seems that there is a readiness to perform maternal care that overrules the recognition system. We describe oviposition behavior and compare it with other descriptions in the literature. Seven behavioral characters related to eggsac building and/or guarding are mapped onto available phylogenies. Maternal care behaviors are quite conservative among spiders, useful for the grouping not only of families, but also of higher order ranks.

Keywords: Maternal care, offspring recognition, oviposition, evolution, Sicariidae, *Loxosceles gaucho*

Spiders show varying degrees of maternal care, from the building of an eggsac to oviposition at suitable sites (Suter et al. 1987; Christenson & Wenzl 1980), eggsac guarding (Pollard 1984; Richman & Jackson 1992; Castanho & Oliveira 1997), extended maternal care during the spiderlings' communal life (Morse 1992) including prey supply and regurgitation for feeding the young (Ito & Shinkai 1993; Evans 1998a; Li et al. 1999) and even extreme suicidal care (Evans et al. 1995; Schneider & Lubin 1997; Kim et al. 2000). Maternal care has positive fitness consequences, reducing predation on eggs (Fink 1987) and offspring (Fink 1986; Willey & Adler 1989; Morse 1992), or providing nutrition and consequently enhancing spiderling survival (Kullmann & Zimmermann 1974; Kim et al. 2000).

Spiders with extended maternal care should evolve offspring recognition systems to avoid exploitation by non-relatives. However, there is little evidence of kin recognition among spiders (Clark & Jackson 1994), perhaps because other conditions are necessary for the evolution of offspring discriminating systems. Evans (1998b) suggests that two of these conditions are a high probability of encountering other conspecifics brood, and a low probability of future breeding opportunities.

Loxosceles gaucho Gertsch 1967 is a spider of medical importance whose bites cause necrotic lesions in humans (Jorge et al. 1991). Due to this medical importance, much of its biology is well documented (Rinaldi et al. 1997; Rinaldi & Stropa 1998). *Loxosceles* spp. are active at night, build simple or complex white silk sheet webs covering the substrate (Bücherl 1964), usually in small natural cavities (Bücherl 1962). Species in the genus do not fulfill any of the requirements for the evolution of kin recognition: they lay up to eight egg clutches from a single mating (Galiano 1967), and are solitary (Delgado 1966), showing a low probability of encountering unrelated offspring. In this paper we describe aspects of *L. gaucho* behavior, including oviposition, maternal care, and kin recognition. We also review the literature concerning these characters and discuss the results from a phylogenetic perspective.

METHODS

Sixty-three females (voucher specimens deposited at Butantan Institute, numbers 30064–

30069) were observed from mating to the emergence of the spiderlings (April–December 1999). Each spider was kept in a 30 × 15 × 20 cm glass terrarium, under an external light–dark cycle, in the laboratory. Prey was offered three times/week, alternating between *Gryllus* sp. (Orthoptera), *Tenebrio molitor* larvae (Coleoptera), *Pycnocellus surinamensis* (Blattodea) and *Alphitobius pisceus* larvae (Coleoptera). Newborn *Gryllus* sp. and *Gryllodes sigilattus* (Orthoptera) were offered twice to the spiderlings five and ten days after their emergence from the eggsac. The observation period was terminated 15 days after the spiderlings emerged from the eggsac.

Experimental design.—Two experiments were conducted, one to test the existence of eggsac recognition by the mother (n = 24), and the other to evaluate the existence of maternal care and its fitness consequences (n = 39). In both cases, the mother was left five days with her own eggsac before it was removed for the beginning of the experimental treatment. The spiders spun a delicate covering sheet on the floor of the terraria, and attached the eggsacs into available folded pieces of cardboard paper, which served as retreats. In order to exchange eggsacs between spiders we removed these cardboard retreats from the terraria.

Eggsac recognition: Twenty-four females with eggsacs were divided into pairs, each pair with eggsacs built on the same day. In each pair, one female received back her own eggsac plus the one of the other female (herein considered the "foreign" eggsac). The second female in each pair was merely an eggsac donor.

Maternal care: The females were assigned to one of three experimental treatments, designed to evaluate the effect of maternal care on spiderling survival. Spiders in the "mother-with-own-offspring" group (own, n = 14) received back their own eggsac; this allowed the description of maternal care, and also functioned as a control for the other treatments. In the two remaining treatments, the females were divided into pairs, and each individual received the eggsac from the other in the pair; one female in the pair (adoption group) took care of the eggsac from her paired conspecific (adopt, n = 13) while the other was removed from the terraria (no-care group), leaving the eggsac alone (ncare, n = 12).

Observational scheme.—In all the experimental treatments, the terraria were scanned three times a day (morning, afternoon and night), in three alternate days for each week, from mating to 15 days after the emergence of the offspring. We observed the relative position between spiders and eggsacs, and also the number of appendages touching the eggsac. If the spiders and/or offspring were in activity (ovipositing, foraging) the observational scheme changed to focal and ad libitum, that is, we focused on the active spider(s) until the end of the behavioral bout.

Comparative data.—The comparative information available in the literature allowed the description of 7 behavioral characters (Appendix 1). We mapped these characters onto the family cladogram proposed by Coddington & Levi (1991), modified at the araneid node by means of the cladogram proposed by Scharff & Coddington (1997); only unambiguous optimizations were discussed. We split the family Sicariidae in order to better analyze the genus *Loxosceles*; we also split the family Salticidae in order to distinguish the proposed primitive spartaeines (Jackson & Pollard 1996) from the other salticids.

RESULTS

Eggsac building.—Eggsac building occurred in four phases. First, the spider constructed a silken basal plate on the substrate. A few days later, she layed a gelatinous mass with the eggs on the basal plate, dried this mass by moving her palps and chelicerae, and finally layed a cover plate, composed of two superimposed silken layers. The observed time intervals within the whole reproductive period are presented in Table 1. The time interval from mating to eggsac building varies much more than the time of egg maturation.

Basal plate: The spider fixed dry threads onto the substrate with swinging movements of the abdomen. During the first part of the movement the spinnerets continuously touched the substrate; then they were lifted, describing an arch, just to touch the substrate again, then the movement was re-started in the opposite direction (Fig. 1a). This was repeated many times (Fig. 1b, c, d) until the spider made a small pause, changed the orientation of her body, and performed this whole pro-

Table 1.—Mean time lag (in days) between distinct behaviors performed by the mothers, from mating to the hatching of the spiderlings. Sample size, standard deviation and range are also shown.

First/Second event	*n*	Mean (days)	SD	Range
Mating/basal plate	19	47.4	18.0	24–82
Mating/egg mass (and cover plate)	70	59.6	28.1	21–120
Basal plate/egg mass (and cover plate)	19	1.7	1.4	0–5
Egg mass (and cover plate)/hatching	36	56.7	6.5	45–68

cedure over and over (Fig. 1d) to the completion of a circular sheet with a diameter of approximately 2 cm.

Egg mass: The spider stayed close to the basal plate for approximately two days, at which time she layed the egg mass onto it (Table 1). Initially, she layed a brownish gelatinous mass on the basal plate. This was done with the cephalotorax directed upwards. The spider repeatedly touched this mass with the palps, then with the chelicerae, ventral cephalotorax and ventral abdomen, always in this sequence. Next she layed the eggs in the mass, with a series of rhythmic leg I and II flexions (in one episode we counted 55 flexions); then she paused, rotated the body axis, and repeated this procedure several times (never more than ten times), gradually reducing the frequency of the rhythmic flexions and enlarging the pauses. At the end of this phase, the eggs were clearly visible through the gelatinous mass.

Desiccation: The spider handled the egg mass with the palps and paused with the chelicerae on the eggs for some minutes. Then she rotated and performed this same sequence until a full 360° rotation was completed. In the meantime, the gelatinous mass disappeared, exposing the conically arranged eggs.

Cover plate: Three distinct sequences of movements compose this last eggsac building phase (Fig. 2). First the spider attached silk at two points near the boundary of the basal plate (open dots, Fig. 2a) and at one point over the egg mass (closed dot, Fig. 2a); this small three-attachments cycle was repeated as the spider rotated on the eggsac (Fig. 2b, c, d); at the end of each cycle the spider paused and touched the egg mass with her palps. After a 360° rotation the spider sometimes repeated the whole procedure in the opposite direction. In the next sequence of movements, the spider fixed several times at opposite sides of the boundary of the basal plate (Fig. 3a, b); she

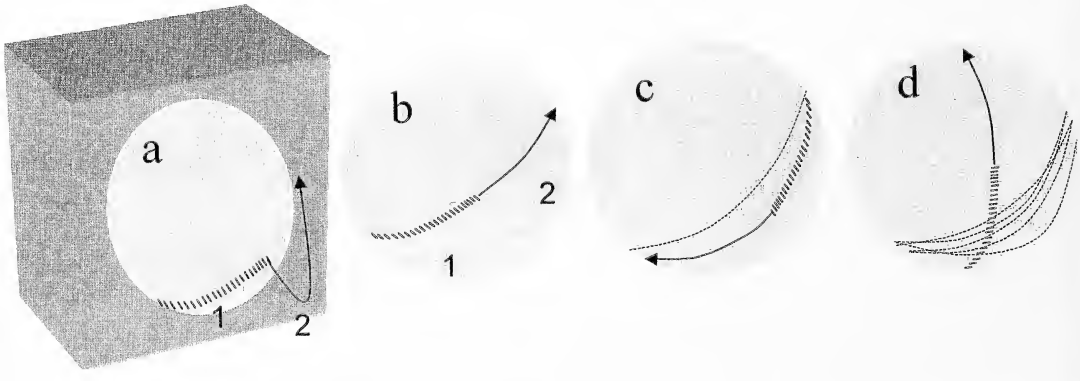

Figure 1.—Building of the basal plate. The spider lays threads (continuous and interrupted black lines) onto the vertical substrate (dark gray). These threads will eventually compose the basal plate (light gray). The spider touches the substrate continuously with the spinnerets during the first part of each movement (1) and then raises the abdomen (2) to touch the substrate again only at the end of the movement (a). These movements are shown in the remaining diagrams without perspective; threads laid in previous movements are depicted as dotted lines; threads currently being laid are shown as in b. After various back and forth movements (c, d) the spider changes the orientation of her body and begins a new back and forth series.

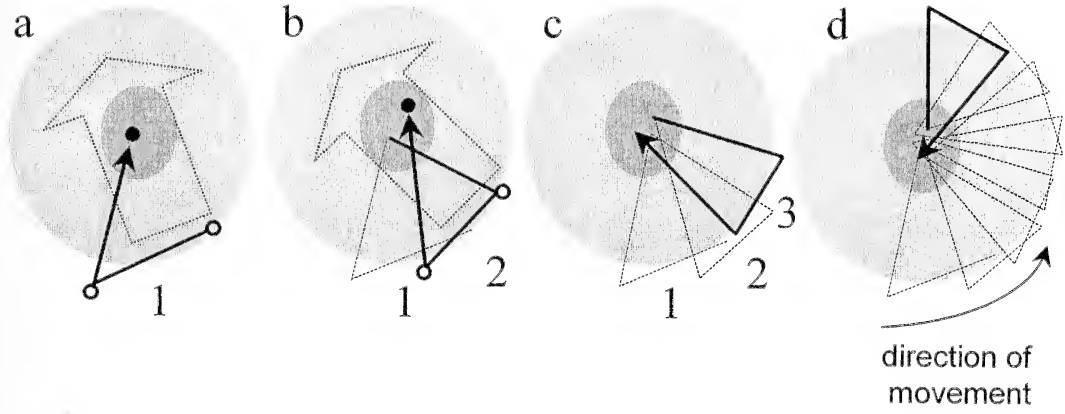

Figure 2.—Building of the first cover plate sheet. The spider lays threads over the basal plate (light gray) and egg mass (dark gray). The large dotted arrow represents the spider body axis (the arrow head is the cephalothorax). The building of this sheet involves the repetition of one same series of movements (1, 2, & 3 in a, b, & c) while rotating the body axis around the whole structure (d); at each movement the spider attaches the current thread in three points, two at the periphery of the basal plate (open dots in a and b), and one over the egg mass (black dot). Dotted lines indicate previous series of movements, and continuous lines indicate current series of movements.

then rotated to initiate a new bout of lateral fixations (Fig. 3c). Small variations in these movements are depicted at Fig. 3d. The spider then increased the amplitude of these lateral fixations, and occasionally scraped the ventral side of her cephalothorax and abdomen with her hind legs, possibly leaving hairs on the silken tissue. Sometimes the spider added small pieces of debris to the cover plate.

Mother-offspring interactions.—The female interacted in various ways with her eggsac. She repaired it, adding lines to the whole structure. She sometimes repositioned it and, in one case, even brought back the egg mass (which had fallen on the terrarium floor) to its original place, adding a new cover plate. A few days before the emergence of the spiderlings the mother made an aperture in the eggsac and began to knock persistently at the cover plate, hitting at it with the tip of her forelegs (as if signaling to the spiderlings the appropriate moment to emerge); in one case we witnessed the mother holding the aperture while the spiderlings abandoned the eggsac.

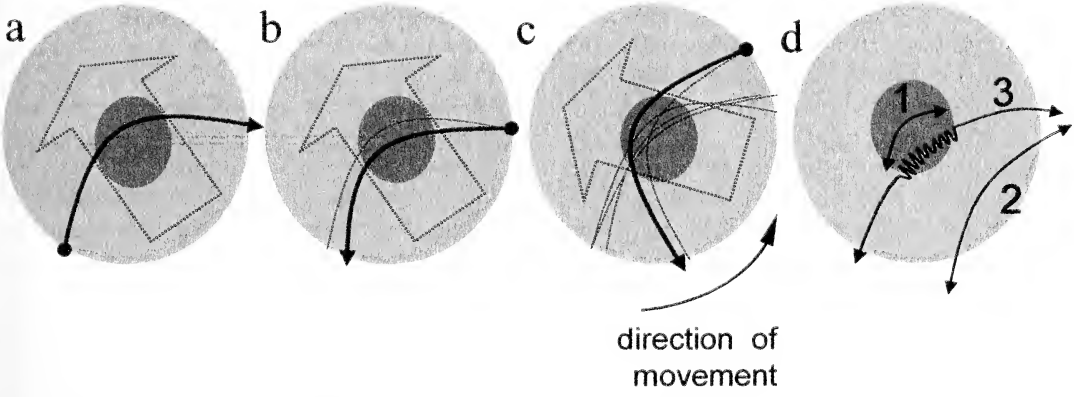

Figure 3.—Building of the second cover plate sheet. The spider makes various back and forth movements (a & b) before changing the body axis to restart this same series in another position (c). These back and forth movements may vary as to the fixation points (d), which can occur near the egg mass (1) or outside the basal plate (2); sometimes the spider slows down the movement while passing over the egg mass and attaches variously onto it (3).

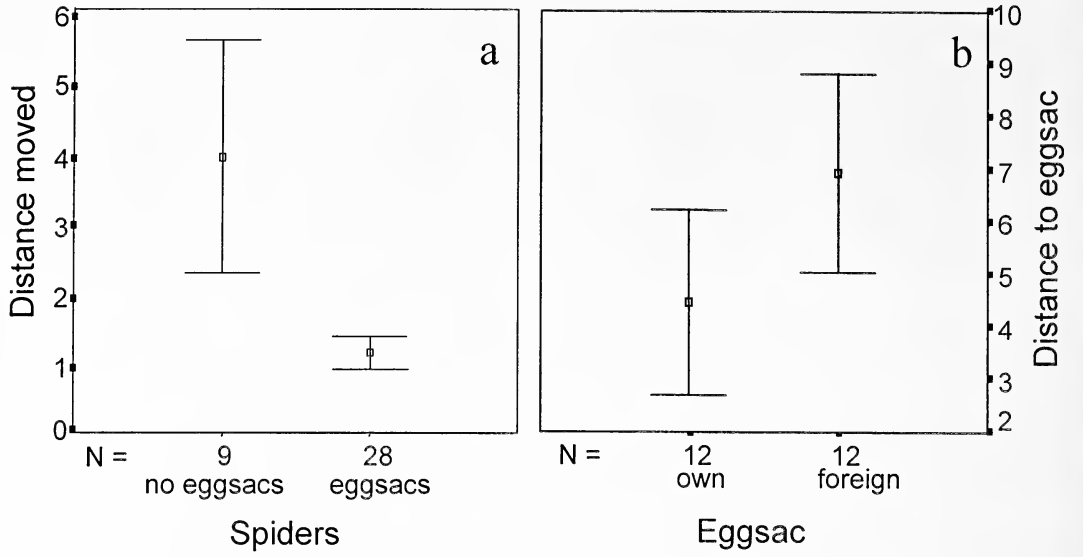

Figure 4.—Maternal displacement and eggsac recognition. Spiders without eggsacs move for larger distances than spiders with eggsacs (cm, mean ± 2SE; 4a). Spiders with eggsacs stay nearer to their own than to foreign eggsacs (cm, mean ± 2SE; 4b).

The female appeared to compete with her offspring for food. Jerking the web repeatedly with her front legs, she appeared to signal to the spiderlings her precedence over a prey item; she also actively pushed nearby spiderlings, or even departed carrying the prey item. Despite that, some spiderlings fed along with the mother.

Offspring-offspring conflicts over prey usually resulted in a behavioral arms race: first they elevated their forelegs, next they beat each others cephalothorax with these legs, and finally they bit each other until one of them fled. Notwithstanding this aggressiveness, the winner often accepted the approach of its siblings after he/she had consumed part of the prey, so that collective feeding among siblings was frequent.

Maternal investment and fitness consequences: After building their eggsac the spiders became much more sedentary, moving only a few centimeters between observations (Fig. 4a, $U = 21$, $P < 0.001$, $n = 37$). It made no difference whether the spider took care of her own or an adoptive eggsac: in either case she stayed equally near it ($Z = -.679$, $P = 0.497$, $n = 27$). Furthermore, the females in the *own* group did not differ in any aspect of maternal care from the ones in the adopt group, either in the number of legs touching the eggsac ($Z = -.776$, $P = 0.438$, $n = 27$) or in the frequency ($Z = -1.165$, $P = 0.244$, $n = 27$) or amplitude ($Z = -.437$, $P = 0.662$, $n = 27$) of their movements in the terrarium.

There was no significant influence of the presence and kind of maternal care on the frequency of successful eggsacs ($\chi^2 = .559$, $P = 0.756$, $n = 39$). Spiderlings in all treatments (own, adopt and ncare) did not differ, on the time of emergence from the eggsac ($\chi^2 = .991$, $P = 0.609$, $n = 28$) or on their total weight ($\chi^2 = .941$, $P = 0.625$, $n = 27$) or survival rate ($\chi^2 = 1.260$, $P = 0.533$, $n = 33$). This may be due to the absence of enemies in laboratory conditions, and experiments under natural environments are necessary to complement these results.

Eggsac recognition.—Although *L. gaucho* treated her own and foreign eggsacs similarly (as shown above), she discriminated between them. When simultaneously offered two eggsacs the spider stayed closer to her own than to the foreign eggsac (Fig. 4b; $t_{2,22} = -1.911$, $P = 0.034$).

Choosing between her own and foreign eggsacs is not an all-or-nothing process: the spider frequently oscillated between the eggsacs for a variable period before settling for one or the other (Fig. 5a, c). Many factors seem to interfere in this process. The spider is able to detect eggsac viability: if one of the eggsacs is not viable ($n = 4$), the spider usu-

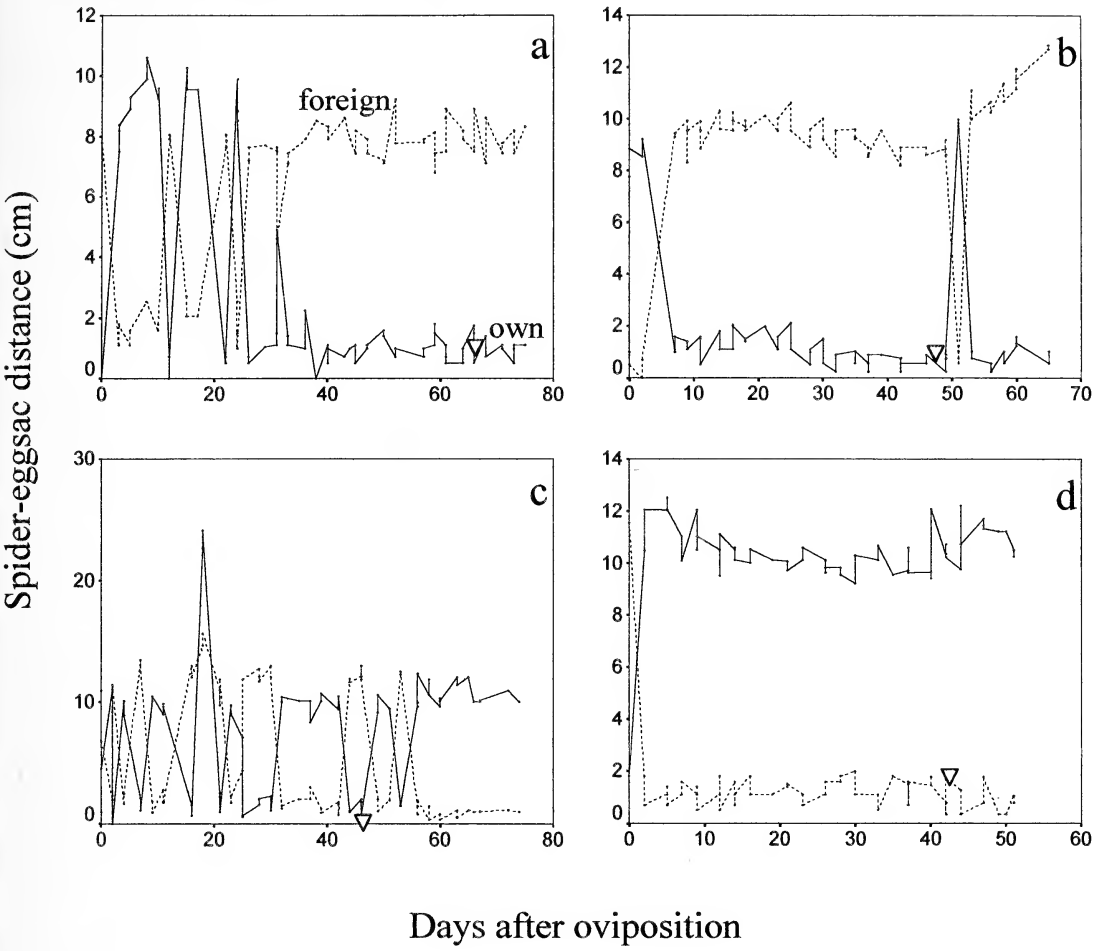

Figure 5.—Oscillations between own and foreign eggsacs. Exposed to her own and a foreign eggsac, the mother frequently oscillated between them, staying sometimes nearer to her own eggsac, and sometimes nearer to the foreign eggsac. The figure depicts the displacement of four spiders (a, b, c, d) in the eggsac recognition experiment. The distance between the spider and each of the eggsacs in the terrarium is shown throughout the experimental period. Continuous line = distance to own eggsac; dotted line = distance to foreign eggsac. Light gray triangles point to the moment of the oviposition of a second eggsac by the mother (from this moment on there are three eggsacs into the terraria); if the triangle is placed onto the dotted line, the new eggsac is close to the foreign eggsac, and vice versa.

ally chooses the other (n = 3), even if the other is the foreign eggsac (Fig. 5d). When the spider lays a new eggsac, she preferentially attends this new eggsac, regardless of where she placed it: near her own old eggsac or near the foreign eggsac. In some cases the spider may visit the foreign eggsac just to open it, helping the spiderlings to emerge, returning afterwards to the original one (Fig. 5b).

DISCUSSION

There are few reports of kin recognition among spiders, and it has been suggested that this recognition is more likely to appear within species that show high levels of maternal investment, breed only once and present high probability of encountering unrelated offspring (Evans 1998b). Although these conditions may enhance the probability of the evolution of recognition systems, they are not necessary conditions for it, since we have found eggsac recognition in *L. gaucho* (Fig. 4b), a species that does not meet these requirements. *L. gaucho* does not show high levels of maternal investment: the female maintains foraging activities throughout the

entire egg-guarding phase, and does not actively feed the young. She breeds many times during her lifetime (in the present study, some spiders laid up to three eggsacs in a 9 month period). Also, this spider has a reduced probability of encountering conspecific offspring during the egg-guarding phase, since a female reduces activity level after building her eggsac (Fig. 4a) and, at least in the Butantan Institute woods, *L. gaucho* specimens are solitary. They are found mainly under dead fallen palm tree leaves, usually one per 1.5m long leaves, sparsely distributed in the forest litter (Kashimata, pers.com.).

Detailed studies of the structure and dynamics of natural populations of *L. gaucho* are necessary in order to evaluate the probability of encountering conspecific offspring, since inter-individual distances may vary as a function of environmental factors and previous experience (Cangialosi & Uetz 1987), so that spatial strategies may change from one population to another.

Readiness for maternal care and cues to eggsac recognition.—If female *L. gaucho* recognize their own eggsac, why should the females adopt conspecific eggsacs? Roland et al. (1996) show that adult, virgin *Coelotes terrestris* Wider 1834 females (Agelenidae) may adopt conspecific offspring in the presence of newborn spiderlings, demonstrating the existence of a readiness to provide maternal care. This readiness could explain adoption by *L. gaucho* females of a single foreign eggsac (adopt group).

Nevertheless, this readiness could not explain adoption in the group of females with two eggsacs: they should always prefer their own brood. They should not oscillate between their own and foreign eggsacs (cf. Fig. 5). Clark & Jackson (1994) showed that *Portia labiata* Thorell 1887 (Salticidae) recognizes her offspring based not only on cues from the eggsac (possibly chemical cues in the silk), but also on cues from the web itself: spiders in foreign webs destroy foreign eggsacs more frequently than spiders in their own webs. It seems from our data that web characteristics are not only important factors in the recognition system, but that they are more important than eggsac factors. If eggsac characteristics were predominant factors in maternal care decisions, *L. gaucho*, confronted with her own and foreign eggsacs, should always prefer her own brood. Conversely, if web characteristics were predominant, both eggsacs would seem rather similar, so that the spider could oscillate between them (Fig. 5).

We have also observed that *L. gaucho* females add threads to the eggsac. Thread addition could render foreign eggsacs progressively more familiar, and this familiarity could explain the otherwise aberrant behavior of some females (Fig. 5b) that go to the foreign eggsac just to open it, facilitating the emergence of the spiderlings.

If eggsac recognition is based on chemical cues in the silk, there may be no specific brood recognition system. The female could only discriminate between familiar and foreign silk, whatever the location of the silk. This could explain the existence of eggsac recognition in a spider that does not present the ecological features usually related to the evolution of kin recognition systems.

Comparative data on the building of eggsacs.—Spiders within the genus *Loxosceles* build their eggsacs in a very similar way. *Loxosceles intermedia* Mello-Leitão 1934 and *L. laeta* Nicolet 1849 all follow the basal-plate/egg-mass/cover-plate sequence, presenting a conical egg mass and a cover plate with two silken layers (Fischer 1996; Galiano 1967).

Despite these similarities, there are some differences between species. For example, this is the first report of a *Loxosceles* species that scrapes her ventral abdomen and cephalothorax while building the last layer of the cover plate. Also, *L. rufipes* Lucas 1834 stays inside an eggsac nest during the egg-guarding phase (Delgado 1966); a similar structure has been observed in some *L. intermedia* (Fischer 1996), but not in *L. laeta* or *L. gaucho*. The building of eggsacs by *L. intermedia* has been described in some detail, and it differs from *L. gaucho* in two additional aspects: she builds the basal plate with movements similar to the building of the first cover plate layer in *L. gaucho* (Fig. 2); besides this, *L. intermedia* lays the egg mass right after the building of the basal plate (cf. Table 1).

Eggsac building has been described for many spider species, but the descriptions vary strongly as to the details included. Despite this variation, the literature reveals a consistent behavioral sequence pattern: most spiders spin a

basal plate, deposit the egg mass over it, and finally spin a cover plate.

Although this sequence might seem a logical one, there are exceptions to the rule which show that this is not a necessary sequence. *Ariadna bicolor* Hentz 1842 does not build either a base or a cover sheet over her eggs; instead this spider builds a closed, silken nest; inside this nest, she secretes a mucous fluid from the oral region, which gradually turns into a gelatinous sheet adhered to the ventral surface of her body; she then deposit her eggs onto this sheet, and stays close to it in the nest, until the emergence of the spiderlings (Montgomery 1909). *Peucetia viridans* Hentz 1832 (Oxyopidae) builds the basal plate and the cover plate (this last one with an opening in the bottom), and only then lays the egg mass into the empty space, sealing the aperture afterwards (Randall 1977; Whitcomb 1962; Whitcomb et al. 1966). Some spiders, like *Pholcus opilionoides* Schrank 1781 (Pholcidae) and the jumping spider *Heliophanus cupreus* Walckenaer 1802 cover the eggs with only a few threads, holding the exposed egg mass with their chelicerae (Pokrowsky 1899; Holm 1940).

A thorough review of the literature shows that eggsac building information is available for at least 60 spider species, scattered through 18 families (Appendix 2). This information was mapped onto available cladograms (Coddington & Levi 1991; Scharff & Coddington 1997) to evaluate the evolution of the behavioral characters.

Evolution of maternal behavior.—The selected behavioral characters (Appendix 1) are quite conservative. Most of them are plesiomorphic within Opisthothelae spiders (Fig. 6), and were subsequently lost or modified in some groups (see discussion below). To our knowledge, there is no information on maternal behavior of liphistiids (Mesothelae), the outgroup of Opisthothelae, which prevents any generalization of the present analysis to Araneae.

Eggsac nests (character 1) have appeared independently at least three times (*Ariadna bicolor*—Segestriidae, gnaphosids, and among non-spartaeineae salticids, Fig. 6). Structurally, gnaphosid nests are similar to the ones of *A. bicolor* (a silken tube closed all around) and different from salticid nests, which are composed of two interconnected silken sheets, usually spun between leaves (Montgomery 1909; Holm 1940; Jackson 1986, 1990a; Hallas & Jackson 1986). The apomorphic presence of eggsac nests among non-spartaeine salticids gives support to the idea that sparteaineae are basal salticids as suggested by Jackson & Pollard (1996).

The sequence base/eggs/cover (character 2) is basal to the whole clade, and disappeared once (*A. bicolor*, Segestriidae, Montgomery 1909). As discussed above, *P. viridans* (Oxyopidae) shows a singular base/cover/eggs/sealing eggsac building sequence (Randall 1977); nevertheless, her "cover" should be considered a remarkable, large marginal wall. There is a striking similarity between the building of *Peucetia*' "cover" (Whitcomb 1962; Whitcomb et al. 1966) and the building of marginal walls in other spiders (for example, *Rabidosa punctulata* Hentz 1844, Montgomery 1903 or *Castianeira longipalpa* Hentz 1847, Montgomery 1909), all of them performed with the same up and down looped strokes of the tip of the abdomen, applied to the circular edge of the basal plate in a clockwise or counter-clockwise direction (while the tips of the palps are pressed against the opposite margin of the basal plate). Therefore the comparative analysis shows, on the basis of this special similarity of movements (Wenzel 1992), that these supposedly distinct structures are indeed the same, homologous structures, distinct only in size.

The use of a silken sheet as a base for the cocoon (character 3) is the plesiomorphic state of this character among Opisthothelae. On this silken sheet there can sometimes exist a cushionlike mat of silk, which can be more or less pronounced in different species. Theridiids have discarded the sheet to oviposit directly onto this cushionlike mat of silk (Montgomery 1903), a putative synapomorphy to the family. Unfortunately the available descriptions do not allow a clear distinction between a single-sheet basal plate and one with both the single-sheet and the mat of silk. Detailed observations are necessary to split this state and further analyze the evolution of this character.

The presence of a marginal wall surrounding the basal plate (character 4) is also plesiomorphic for Opisthothelae, but this character disappeared independently at least 5 times (Fig. 6). The marginal wall is extremely

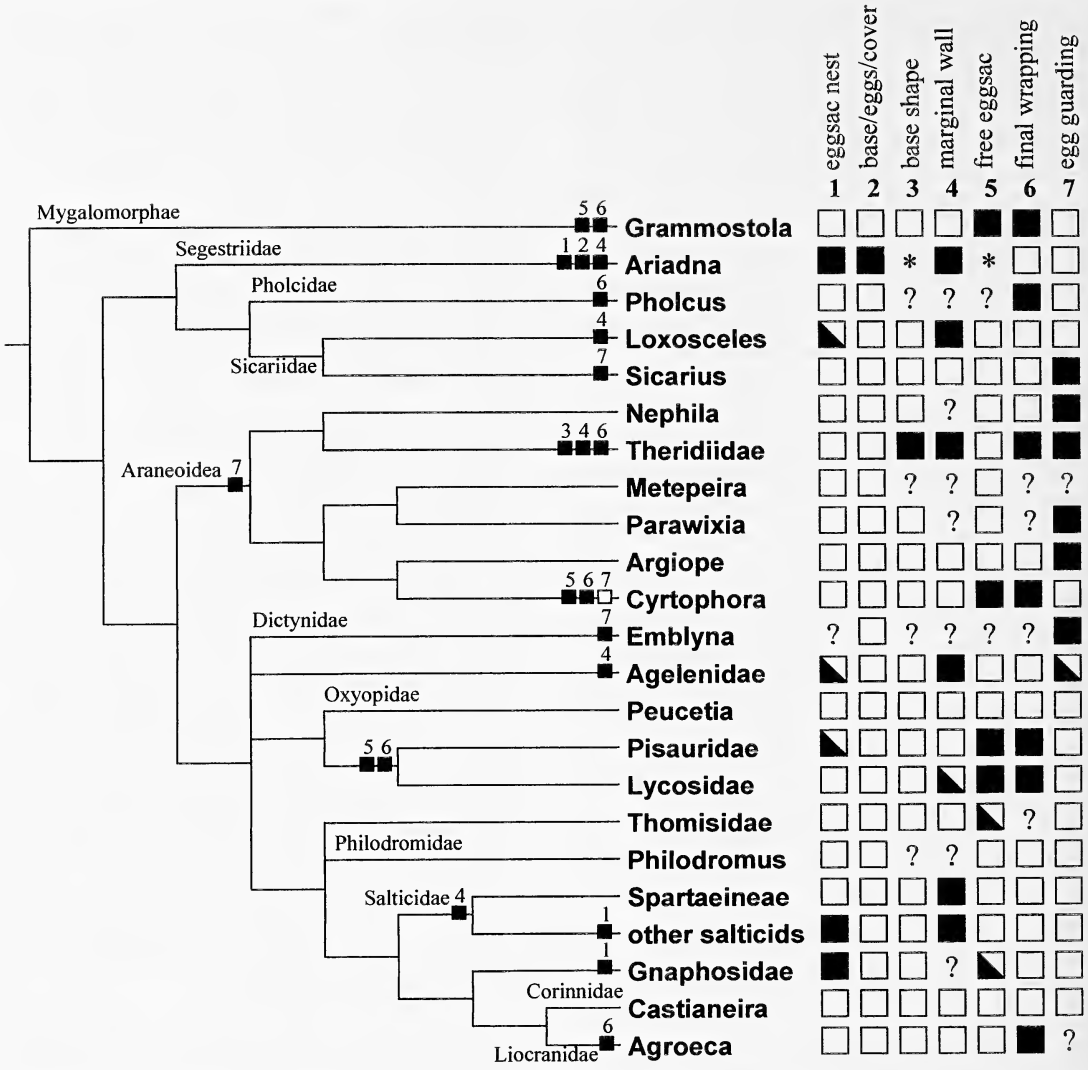

Figure 6.—Probable evolution of maternal behavioral characters among Opisthothelae. Data on Appendix 2 were mapped onto the family cladogram proposed by Coddington & Levi (1991), modified at the araneid node by means of the cladogram proposed by Scharff & Coddington (1997). ■ = synapomorphy; □ = plesiomorphy or reversion; ◪ = polymorphism; "?" = unknown; "*" = nonapplicable.

variable in size, ranging from 1.5 cm high in *P. viridans* (Randall 1977) to a subtle, almost imperceptible ridge in *Schizocosa crassipes* Walckenaer 1837 (Montgomery 1903). In this last case, some authors may have simply overlooked this delicate feature, and it is possible that more careful observations will reveal its existence in many more taxa, thus reducing the level of homoplasy in this character.

After covering the eggsac, some spiders detach it from the substrate (character 5) and wrap it all around (character 6). These characters have appeared simultaneously and independently in three taxa: among mygalomorph spiders [they also occur in *Vitalius sorocabae* Mello-Leitão 1923 (HFJ, pers.obs.)], in *Cyrtophora moluccencis* Doleschall 1857, and at the node Pisauridae plus Lycosidae (Bücherl 1951; Berry 1983; Montgomery 1903, 1909). If a spider detaches the eggsac from the substrate, she will also wrap it afterwards, but the reverse is not true: theridiids and liocranids (*Agroeca brunnea* Blackwall 1833) wrap the eggsac while it is still

hanging from the upper substrate (Montgomery 1903; Ewing 1918; Bonnet 1935; Holm 1940).

Although egg guarding (character 7) is a plesiomorphic behavior for Opisthothelae, it has been lost at least three times, and its absense is a putative synapomorphy for a large group of families, the araneoids. These web building spiders may place the eggsac either far from or near their web, sometimes even at the periphery of the trap, but usually do not maintain close, persistent contact with it as other spiders do (Montgomery 1903; Bonnet 1925, 1935; Austin & Anderson 1978; Gobbi et al. 1979). Since uloborids, the outgroup of araneoids (Griswold et al. 1998), still preserve the plesiomorphic egg guarding behavior [*Miagrammopes animotus* Chickering 1968 guards her eggsac until the emergence of the spiderlings (Opell 2001)], it is possible that this behavior has been lost at the araneoid node.

This analysis reveals that maternal behavioral characters are conservative among Opisthothelae, useful for the grouping not only of families, but also of higher order ranks, such as araneoids and Pisauridae plus Lycosidae. It is surprising that behavioral characters, frequently considered labile features to be avoided in phylogenetic contexts (Atz 1970; Brown 1975), present such a conservative evolutionary pattern. Nevertheless, the hypotheses herein discussed about the evolution of behavioral characters are based on a still scattered database: many families are not included in the analysis, or are represented by just a few species. Furthermore, it must be clear that such hypotheses are always just as good as the phylogenies they rely on, because changes in the cladistic structure entail changes in the evolutionary hypotheses (Ryan 1995). Maternal behaviors have proved to be useful at the phylogenetic level, but much work is necessary to gather enough information for a comprehensive analysis within Araneae.

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APPENDIX 1.

Description of behavioral characters and definition of character states.

Character 1. Nest for the eggsac: (0) absent; (1) present. There is considerable structural variation among nests; as a rule they are built before eggsac construction, and they are larger than the female. Salticids usually present open nests, with one to many ways out; gnaphosids and segestriids build closed nests, and stay in them until the emergence of the spiderlings. Despite the variations in nest structure, all of them had at least an upper and a lower substrate, usually made up of silken sheets [but see Jackson (1986) for a nest almost without silk, between two leaves, built by the spider *Thiana demissa* Thorell 1892].

Character 2. General eggsac building sequence: base/oviposition/cover; (0) absent; (1) present. This is a widespread character: the spider starts building a base silken sheet, deposits the eggs onto it and builds a silken cover sheet onto the egg mass. This character was scored as present if these three steps were all present, and were performed in this order, notwithstanding the existence of intermediate steps, like the building of a silken wall (see below) onto the base, before egg-laying.

Character 3. Shape of the base: (0) silken sheet, sometimes with a cushionlike mat of curled strands of silk; (1) cushionlike mat of curled strands of silk. Most spiders present the single sheet state of the character.

Character 4. Marginal wall: (0) absent; (1) present. After building the basal plate, some spiders spin at its perimeter a wall of curled loops of silk. This is built with up and down movements of the abdomen, while the spider slowly rotates her body and touches the opposite side of the basal plate with the tip of the palpi. This silken wall can be a clearly visible structure (as in *Sicarius* sp., Levi & Levi 1969), but it is sometimes rather difficult to see. We only scored this character as present when explicitly described by the author or clearly distinguishable in pictures or photographs.

Character 5. Free eggsac from substrate: (0) no; (1) yes. After building the cover plate, some spiders remove the whole structure from the substrate with legs I and/or chelicerae. Species that have the eggsac firmly adhered to the substrate pull the basal plate from the substrate with legs I. Species that hang the eggsac from the web merely cut the suspension threads with the chelicerae. Once the eggsac has been removed from the substrate, the spider handles it freely with legs II, III and IV.

Character 6. Final eggsac wrapping: (0) absent; (1) present. After covering the eggmass with a sheet of threads (cover plate), some spiders envelop the whole structure (basal plate included) with a final silken protection. Note that the cover plate never enwraps the whole structure, but is built over the basal plate and eggmass. This behavior may be somewhat simplified in some taxa, as is the case for *Pardosa lapidicina* Emerton 1885, which wraps only the junction between the cover and the basal plate (Eason 1969).

Character 7. Eggsac guarding: (0) absent; (1) present. This behavior varies strongly, for the spider may carry the eggsac on the chelicerae (like pholcids), on the spinnerets (like lycosids) or may not carry it at all, in which case she may stay continuously in touch with it until the emergence of the spiderlings, or even make foraging trips and then return to the eggsac. For the sake of simplicity, and due to the incompleteness of many descriptions, we decided to score all these instances merely as the presence of eggsac guarding behavior.

APPENDIX 2.
Matrix of spider species versus characters for maternal behaviors.

If the species name has changed, the old name is also cited. Only species for which there is information on at least 2 characters were included. Data were compiled based mainly on original descriptions and, in a few cases on informative illustrations. Character 1 = eggsac nest; character 2 = base/eggs/cover building sequence; character 3 = base shape; character 4 = marginal wall; character 5 = free eggsac from substrate; character 6 = final wrapping; character 7 = eggsac guarding. See Appendix 1 for character descriptions and definitions of states. "?" = unknown; "*" = nonapplicable; "v" = polymorphism.

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Species (previous name, if changed)	Family	1	2	3	4	5	6	7	Reference
Agelena labyrinthica Clerck 1757	Agelenidea	1	1	0	?	0	0	1	Warburton 1891
Tegenaria domestica Clerck 1757 (*T. derhami*)	Agelenidae	0	1	0	0	0	0	0	Montgomery 1903
Araneus quadratus Clerck 1757	Araneidae	0	1	0	1	?	1	?	Crome 1956
Argiope bruennichi Scopoli 1772	Araneidae	0	1	0	1	0	0	0	Bonnet 1925
Cyrtophora moluccensis Doleschall 1857	Araneidae	0	1	0	1	1	1	1	Berry 1983
Larinioides cornutus Clerck 1757 (*Epeira strix*)	Araneidae	0	1	0	?	?	?	?	Emerton 1877
Metepeira labyrinthea Hentz 1847 (*Epeira labyrinthea*)	Araneidae	0	1	?	?	0	?	?	Montgomery 1903
Prawixia bistriata Rengger 1836 (*Eriophora bistriata*)	Araneidae	0	1	0	?	0	?	0	Gobbi et al 1979
Castianeira longipalpa Hentz 1847 (*Geotrecha pinnata*)	Corinnidae	0	1	1	1	0	0	1	Montgomery 1909
Emblyna sublata Hentz 1850 (*Dyctina volupis*)	Dictynidae	?	1	?	?	?	?	0	Montgomery 1903
Drassodes neglectus Keyserling 1887	Gnaphosidae	1	1	?	?	1	?	1	Montgomery 1909
Sergiolus capulatus Walckenaer 1837 (*Poecilochroa variegata*)	Gnaphosidae	1	1	?	?	0	0	1	Montgomery 1909
Zelotes ater Hentz 1832 (*Herpyllus ater*)	Gnaphosidae	1	1	0	?	?	?	1	Emerton 1877
Agroeca burnnea Blackwall 1833	Liocranidae	0	1	0	1	0	1	?	Holm 1940
Pardosa amentata Clerck 1757	Lycosidae	0	1	0	?	1	1	1	Montgomery 1903
P. lapidicina Emerton 1885	Lycosidae	0	1	0	1	1	1	1	Eason 1969
P. milvina Hentz 1844 (*P. nigropalpis*)	Lycosidae	0	1	0	0	1	1	1	Montgomery 1903
Rabidosa punctulata Hentz 1844 (*L. punctulata*)	Lycosidae	0	1	0	1	1	1	?	Montgomery 1903
Schizocosa ocreata Hentz 1844 (*L. ocreata*)	Lycosidae	0	1	0	1	1	1	1	Montgomery 1903
S. avida Walckenaer 1837 (*L. lepida*)	Lycosidae	0	1	0	1	1	1	1	Montgomery 1903
S. crassipes Walckenaer 1837 (*Lycosa stonei*)	Lycosidae	0	1	0	1	1	1	1	Montgomery 1903
Peucetia viridans Hentz 1832	Oxyopidae	0	1	0	1	0	0	1	Whitcomb 1962; Whitcomb et al. 1966
Philodromus aureolus Clerck 1757	Philodromidae	0	1	?	?	0	0	1	Montgomery 1903
Pholcus opilionoides Schrank 1781	Pholcidae	0	1	?	?	?	1	1	Pokrowsky 1899
Dolomedes fimbriatus Clerck 1757	Pisauridae	1	1	0	1	?	?	?	Pappenheim 1903 (apud Montgomery 1909)
Pisaurina mira Walckenaer 1837	Pisauridae	v	1	0	?	1	1	1	Montgomery 1909
Heliophanus cupreus Walckenaer 1802	Salticidae	1	?	?	?	?	?	1	Holm 1940
Marpissa muscosa Clerck 1757 (*M. rumpfii*)	Salticidae	1	1	0	?	0	?	1	Holm 1940
Phidippus purpuratus Keyserling 1885	Salticidae	1	1	?	?	0	0	1	Montgomery 1909
Thiania demissa Thorell 1892	Salticidae	1	1	0	?	0	0	1	Jackson 1986

Appendix 2.—Continued.

Species (previous name, if changed)	Family	1	2	3	4	5	6	7	Reference
Thiania sp.	Salticidae	1	1	0	?	0	0	1	Jackson 1986
Brettus cingulatus Thorell 1895	Salticidae	0	1	0	0	0	0	1	Jackson & Hallas 1986a
Cocalus gibbosus Wanless 1981	Salticidae	0	1	0	?	0	0	1	Jackson 190b
Cyrba algerina Lucas 1846	Salticidae	?	1	0	0	0	0	?	Jackson & Hallas 1986a
Gelotia sp.	Salticidae	0	1	0	?	0	0	1	Jackson 1990c
Portia fimbriata Doleschall 1859	Salticidae	0	1	0	0	0	0	1	Jackson & Hallas 1986b
Portia labiata Thorell 1887	Salticidae	0	1	0	0	0	0	1	Jackson & Hallas 1986b
Asemonea murphyae Wanless 1980 (*A. murphyi*)	Salticidae	1	1	0	?	0	0	1	Jackson 1990a
Asemonea tenuipes Cambridge 1869	Salticidae	1	?	0	?	0	0	1	Hallas & Jackson 1986
Goleba puella Simon 1885	Salticidae	1	1	0	?	0	0	1	Jackson 1990a
Lyssomanes patens Peckham & Peckham 1896	Salticidae	1	1	0	?	0	0	1	Jackson 1990a
Lyssomanes sp. 1	Salticidae	1	1	0	?	0	0	1	Jackson 1990a
Lysssomanes sp. 2	Salticidae	1	1	0	?	0	0	1	Jackson 1990a
Lyssomanes viridis Walckenaer 1837	Salticidae	1	1	0	0	0	0	1	Hallas & Jackson 1986
Onomastus nigricaudus Simon 1900 (*O. nigricauda*)	Salticidae	1	1	0	?	0	0	1	Jackson 1990a
Tomocyrba holmi Prószynski & Zabka 1983 (*Onomastus holmi*)	Salticidae	1	1	0	?	0	0	1	Jackson 1990a
Ariadna bicolor Hentz 1842	Segestriidae	1	0	*	0	*	0	1	Montgomery 1909
Loxosceles gaucho Gertsch 1967	Sicariidae	0	1	0	0	0	0	1	Present paper
L. intermedia Mello-Leitão 1934	Sicariidae	0	1	0	0	0	0	1	Fischer 1996
L. laeta Nicolet 1849	Sicariidae	0	1	0	0	0	0	1	Galiano 1967
L. rufipes Lucas 1834	Sicariidae	1	?	?	?	?	?	1	Delgado 1966
Sicarius sp. 1	Sicariidae	0	1	0	1	0	0	0	Levi & Levi 1969
Nephila edulis Labillardière 1799	Tetragnathidae	0	1	0	?	0	0	0	Austin & Anderson 1978
Grammostola actaeon Pocock 1903	Theraphosidae	0	1	0	1	1	1	1	Bücherl 1951
Grammostola mollicoma Ausserer 1875 (*G. longimana*)	Theraphosidae	0	1	0	1	1	1	1	Bücherl 1951
Achaeraranea tepidariorum Koch 1841 (*Theridion tepidariorum*)	Theridiidae	0	1	1	0	0	1	0	Montgomery 1903; Ewing 1918; Bonnet 1935
Enoplognatha marmorata Hentz 1850 (*Steatoda marmorata*)	Theridiidae	0	1	?	?	?	?	?	Montgomery 1903
Latrodectus mactans Fabricius 1775	Theridiidae	0	1	?	?	0	?	?	Montgomery 1907
Steatoda triangulosa Walckenaer 1802 (*Teutana triangulosa*)	Theridiidae	0	1	1	0	0	1	0	Montgomery 1903
Thomisus onustus Walckenaer 1805	Thomisidae	0	1	0	1	1	?	1	Fabre 1823
Xysticus ferox Hentz 1847 (*Xysticus stomachosus*)	Thomisidae	0	1	?	?	0	?	1	Montgomery 1903

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PROBLEM SOLVING IN THE SPIDER FAMILIES MITURGIDAE, CTENIDAE AND PSECHRIDAE (ARANEAE) IN AUSTRALIA AND NEW ZEALAND

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ABSTRACT. The genus *Uliodon* L. Koch is reviewed. It now includes only the type species, *Uliodon albopunctatus* L. Koch 1873, *Uliodon cervinus* L. Koch 1873, and *Zora frenatus* Koch 1873, and the genus is transferred to the Zoropsidae. *Uliodon* is known only from New Zealand. Through an original misreading of the type specimen locality data, both species were erroneously reported from Australia. Forster and Homann previously referred to *Uliodon* species as *Miturga*, which is endemic to Australia. The subfamily Uliodoninae Lehtinen 1967 was founded on the characters of *Zora tarantulina* L. Koch 1873, later transferred to *Uliodon* by Simon. The diagnostic character of the subfamily, the very long path of the embolus, is not found in *Uliodon*. The subfamily is here diagnosed from the genus; its validity is unclear. In any case, both *Uliodon* and Uliodoninae are transferred to the Zoropsidae along with the Australian *Huntia* Gray & Thompson 2001. *Zora tarantulina* is made the type species of a new monotypic genus, *Mituliodon*, included in the Miturgidae; the genus is known only from Australia and Timor. *Mituliodon tarantulinus* (L. Koch 1873) now newly includes in its synonymy, *Uliodon australiensis* (L. Koch 1873), *Uliodon torvus* (L. Koch 1873), *Miturga maculata* Hogg 1900, *Syspira rubicunda* Hogg 1900 and *Miturga velox* Hickman 1930. The New Zealand genus *Zealoctenus* is transferred from the Ctenidae to the Miturgidae because it is very similar to the Australian genus *Diaprograpta* Simon 1909; the other New Zealand "ctenid" genus, *Nemoctenus* Forster & Wilton 1973, along with the Australian zorid *Horioctenoides* Main 1954 are synonymized with the zorid genus *Argoctenus* L. Koch 1878, found in Australia, New Zealand and New Caledonia. The New Zealand "psechrids" *Poaka* Forster & Wilton 1973 and *Haurokoa* Forster & Wilton 1973 are transferred to the Amaurobiidae and Tengellidae, respectively.

Keywords: Australasia, Lycosoidea, Miturgidae, Psechridae

In our studies on the Australian Miturgidae, a problem was encountered with New Zealand taxa which Forster (e.g. Forster 1967; Forster & Forster 1973) had considered *Miturga* Thorell 1870. When that New Zealand material was examined and relationships sought, the late Ray Forster (pers. comm.) agreed that although it resembled *Miturga* it was not congeneric. Discerning what exactly constitutes a miturgid has been like the process of peeling a banana. Only by removing the monophyletic outer layers can the integrity and monophyly of the inner fruit (Miturgidae) be established. Raven et al. (2001) began this process with the description of a new ctenid genus, *Amauropelma* Raven et al. 2001, which under existing diagnoses was a miturgid.

The genus *Uliodon* L. Koch 1873 was described for females of two new species, *U. albopunctatus* L. Koch 1873 and *U. cervinus* L. Koch 1873, both reportedly from "New Holland". Later in that monograph, Koch described four new species (including one based on a male, *Zora tarantulina* L. Koch 1873) from Australia and placed them in the Palaearctic (zorid) genus *Zora*. Simon (1897) transferred the subsequent four species of *Zora* C.L. Koch 1847 into *Uliodon* (*Z. tarantulina*, *Z. australiensis*, *Z. torva* and *Z. ferruginea*), a transfer that has not since been contested. Lehtinen (1967) transferred *Uliodon* into the Miturgidae and raised a new subfamily based on the "exceptional course of the embolus" of the male palp of *Uliodon tarantulinus*. Recently, Griswold (1993) formed a cladogram using *Uliodon tarantulinus* as the exemplar for the Miturgidae.

Hence, although unrevised, the genus *Uliodon* has been used in two major phylogenetic studies (Lehtinen 1967; Griswold 1993). In the latter, it was the sole representative of the Miturgidae. Spiders heretofore assigned to

Uliodon in Australia are widespread and active hunters in leaf litter through coastal Australia. In our present studies on the Australian Miturgidae, we could find only one species of *Uliodon*, that figured by Griswold (1993) as *U. tarantulinus* (L. Koch). At the conclusion of the study, we examined the types of *Uliodon*, *U. albopunctatus* (the type species), and *U. cervinus*, in what we thought would be a confirmatory check. The types of both *U. albopunctatus* and *U. cervinus* are females and could not be matched morphologically with any Australian spider genus in the Miturgidae or other families. They lack both true claw tufts and a third claw but have a good scopula as in *Miturga*. Females differ from those of *Miturga* in the epigyne and the spigots on the PMS. We did, however, find material matching the type material of both species only in New Zealand. When males matching the females of *U. albopunctatus* and *U. cervinus* were recognized from New Zealand, even more differences between *Uliodon* s. strict. and *Miturga* were noted. Neither species originally placed in *Uliodon* by Koch is con-familial with *Uliodon tarantulinus*. Griswold (1993) was, nevertheless, correct in considering *Uliodon tarantulinus* as a miturgid and although the genus name is incorrect, his cladistic analysis is unaffected by this realization.

The *Uliodon* problem clearly began with conflicts in locality data with the types of *U. albopunctatus* (type species) and *U. cervinus*. Koch (1873: 433) listed them both as "Neu Holland". However, the types (from NHMW) are labelled 'Neuseeland: "NOVARA"-Reise; Hochstetter don.', and 'Neu-Holland (Australien): "NOVARA"-Reise; Hochstetter don.', respectively. That is, they were collected on the voyage of the vessel *Novara* and donated by Hochstetter. Hochstetter collected exclusively in New Zealand. The apparently conflicting labels may have lead Koch to assume the material was from Australia. Certainly, the Novara did visit both New Zealand and Australia (Fletcher 1985). However, the material has the same collection data as the types of the New Zealand hexathelid, *Hexathele hochstetteri* Ausserer 1871, also deposited in NHMW. In any case, the morphological data are compelling: *Uliodon albopunctatus* and *Uliodon cervinus* are New Zealand species.

Our current studies also indicated the presence of the Zoropsidae in Australia which further extend the concept of the family. Under that revised diagnosis, the New Zealand *Uliodon* fit well into the Zoropsidae.

Having removed *Uliodon* from the Miturgidae, a new genus is needed for *Zora tarantulina*. The begged question is then: What is a miturgid and are there any in New Zealand? Davies (1986: 35) keyed the Miturgidae by posterior eyes straight or slightly curved, long and conical apical segment of PLS, striped carapace, sheet web, two claws and claw tufts. That character combination does not apply to any known miturgid. *Diaprograpta*, *Mituliodon*, new genera, and most miturgid genera lack the elongate PLS; *Miturga* lacks claw tufts and alone builds a sheet web as a retreat. Raven et al. (2001) showed that those characters were insufficient to correctly place the ctenid genus *Amauropelma* Raven & Stumkat 2001.

Miturgidae are presently best defined by the character combination given below (also see Table 1). The boundary with the Ctenidae has been diffuse (see Raven et al. 2001) and hence it was to the New Zealand ctenids and psechrids (*Zealoctenus* Forster & Wilton 1973, *Nemoctenus* Forster & Wilton 1973, *Poaka* Forster & Wilton 1973) that our attention was drawn. Forster & Wilton (1973) had noted difficulty in applying the concepts of the Ctenidae and Zoridae given by Lehtinen (1967). The diagnosis of the Miturgidae given here fits that of *Zealoctenus*, a monotypic genus founded on a single female. *Nemoctenus* is clearly a zorid.

Poaka has similar eyes, carapace shape and pattern and abdominal stripes to the miturgid *Diaprograpta* and hence was examined. Forster & Wilton (1973) found difficulty in placing both *Poaka* and *Haurokoa* but "dumped" them uneasily into the Psechridae. On examination of fresh material in Lincoln University, New Zealand, it is clear that *Poaka* is an amaurobiid resembling the Australian *Manjala* Davies 1990 with which it shares the cribellum, the numerous strong paired spines on tibiae and metatarsi I, II, retrocoxal hymen and carapace shape and pattern and the abdominal pattern. Hence, *Poaka* is transferred to the Amaurobiidae. Equally, unlike the large tropical psechrids, *Haurokoa* lacks claw tufts and does not build a sheet web but hunts on low vegetation (Forster & Wilton 1973). The simple form of the palpal bulb and strongly

recurved eye group suggest either Ctenidae (cf. *Amauropelma* Raven & Stumkat 2001) or Tengellidae. In having only a weakly curved front row of eyes and three claws without tufts, the Tengellidae seems the most likely placement. Hence, it is to the Tengellidae that *Haurokoa* is tentatively transferred. This paper then clarifies the relationships of what was placed in the Miturgidae, Ctenidae and Psechridae in New Zealand and the resulting problems generated in Australia.

METHODS

Localities.—Cons. Pk. = Conservation Park; ME.Q = mid-eastern Queensland; NE.Q = northeast Queensland; NP = National Park; SE.Q = south-east Queensland; SF = State Forest.

Abbreviations.—ALS = anterior lateral spinnerets; AME = anterior median spinnerets; AME = anterior median eyes; ALE = anterior lateral eyes; PLS = posterior lateral spinnerets; PMS = posterior median spinnerets; PLE = posterior lateral eyes; RTA = retrolateral tibial apophysis; RCH = retrocoxal hymen.

Museums.—NHMW = Naturhistorisches Museum, Wein, Austria; QM = Queensland Museum, Brisbane; WAM = Western Australian Museum, Perth; SAM = South Australian Museum, Adelaide; AMS = Australian Museum, Sydney; CAS = California Academy of Science (CAS), San Francisco; BMNH = Natural History Museum (London); QVM = Queen Victoria Museum, Launceston, Tasmania.

SYSTEMATICS

Family Zoropsidae Bertkau 1882

Zoropsididae [sic.] Bertkau 1882: 337.

Uliodoninae Lehtinen 1967: 316. NEW SYNONYMY.

Diagnosis.—Male Zoropsidae differ from those of Miturgidae in the presence of a dense scopula dorsally on the palpal cymbium, pedal tibiae with basal fracture and the presence of a sclerotized shield on the anterior face of the abdomen. Many female zoropsids have spigots evident dorsally on the posterior median spinnerets but all have strong paired spines on raised bases on tibiae (5–7 pairs) and at least 3 pairs on metatarsi I, II.

Description.—Males with dense scopula dorsally on male palpal cymbium, pedal tibia with basal fracture; tibial apophysis more dorsal than retrolateral; eyes in two recurved rows; 2 or 3 claws; claw tufts present or absent. Cribellum present or absent. Retrocoxal hymen distinct on retrolateral coxae I. Spigots present dorsally on PMS of females (*Zoropsis*, *Uliodon*, *Huntia*); apical PLS short, domed. Femur I, especially of females, with enlarged spine proventrally; at least 5 pairs of strong spines on tibia and 3 pairs on metatarsi I, II ventrally. Trochanters weakly but distinctly notched. Labium wider than long.

Included Genera.—*Zoropsis* Simon 1878 from southeast Asia and Europe; *Takeoa* Lehtinen 1967 from China and Japan; *Uliodon* L. Koch 1873 from New Zealand; and *Huntia* Gray & Thompson 2001 from Victoria and Western Australia; based upon Platnick 1998 with addition of new genera.

Remarks.—Uliodoninae were "characterized by the exceptional course of the embolus in males" (Lehtinen 1967: 317) but that was based on a male that is not confamilial with *Uliodon*. The subfamily diagnosis is hence incorrect. At present, the subfamily includes only *Uliodon* and serves no grouping function and in the absence of a cladogram reflects no indication of higher relationships. Other subfamilies listed by Lehtinen (1967) in the Miturgidae have been re-elevated to families, i.e. Tengellidae, Zoropsidae, or moved to other families Amaurobioidinae (Anyphaenidae). Eutichurinae have been moved to the Clubionidae, back to the Miturgidae and most recently back to the Clubionidae (Deeleman-Reinhold 2001; not accepted by Platnick 2001). Griswold (1991) left the Griswoldiinae (as Machadoninae) unplaced in the Lycosoidea. Lehtinen (1967) included *Uliodon*, the madagascan genera *Uduba* Simon 1880, *Zorodictyna* Strand 1907, *Calamistrula* Dahl 1908, the African genus *Raecius* Simon 1892, and from Baltic Amber, *Adamator* Petrunkevitch 1942 in the Uliodoninae. Griswold (1993) included *Uliodon* in a cladogram of lycosoids but did not formalize any nomenclatural conclusions. Relationships are not here extensively explored. However, character distributions are given (Table 1).

Homann (1971) reported that *Miturga* has a grate-shaped tapetum; in fact, that is true for *Miturga* but Homann's material was not *Miturga*. In the Forster laboratory, I found a letter and photographs by R.R. Forster in which

Table 1.—Diagnostic characters of miturgoid families. Abbreviations: PLS = posterior lateral spinnerets; PMS = posterior median spinnerets; PTF = predistal tarsal fracture; RCH = retrocoxal hymen; RTA = retrotibial apophysis.

	Ctenidae	Zoridae	Zoropsidae	Miturgidae	Tengellidae	Pisauridae	Eutichirinae
RCH	present	present	present	present	present	absent	pres./abs.
PTF	absent	absent	absent	absent	absent	present	absent
Tibial Crack, male	absent	absent	present	absent	absent	absent	absent
Cymbial scopula, male	pres./abs.	absent	present	absent	absent	absent	absent
Leg scopula	strong-absent	absent	strong-absent	strong	absent	absent	absent
Claw tufts	present	pres./abs.	pres./abs.	pres./abs.	pres./abs.	absent	present
Black eye row	recurved-2 rows	strongly recurved-2 rows	straight-recurved	straight-recurved	straight-recurved	strongly recurved-2 rows	procurved
Maxillae, shape	rectanquloid	rectanguloid	rectanguloid	rectanguloid	rectanguloid	rectanguloid	dumbell
Trochanters	notched	notched	notched	notched	notched	notched	unnotched
Claws	2	2	2–3	2	2–3	3	2
Tibial & metatarsal spines 1, 2	strong	strong	strong	weak	weak	weak	strong-weak
PLS, apical segment shape	domed	domed	domed	domed to digitiform	domed	domed	digitiform
PMS female, spigots	apical	apical	dorsal	apical	apical or dorsal	apical	apical
Interlocking lobes, male tegulum	absent	absent	present	absent	present	absent	absent
Autapomorphy	ALE high near PME	combination	male tibiae with basal crack	RTA with unsclerotized region	combination	combination	combination

it was clear that the material sent to Homann labelled *Miturga* was the New Zealand *Uliodon*. Grate-shaped tapeta are also found in the Zoropsidae (Griswold 1993).

Gray & Thompson (2001) described two new lycosoid genera, *Bengalla* Gray & Thompson 2001 and *Huntia* Gray & Thompson 2001. *Bengalla* will be dealt with elsewhere but is here considered to fit Griswold's (1991) concept of the Tengellidae. We have examined material of *Huntia*. Males have the tibial crack, the cymbial scopula, and a sclerotized shield on the anterior face of the abdomen and both males and females have the strong paired spines on tibiae I and II. Females of *Huntia deepensis* Gray & Thompson 2001 have spigots dorsally on the PMS. Also, like other undescribed Australian zoropsids, *Huntia* has a tarsal rod and tegular-subtegular interlocking lobes. Gray & Thompson (2001) considered the longer labium and absence of claw tufts reason to exclude the genus from the Zoropsidae. The labium of *Zoropsis spinimana* (female, BCB colln. examined) is about as long as wide and the character is not considered sufficient to exclude a genus from the family. The absence of claw tufts in *Huntia* simply places it lower on the cladogram than *Zoropsis*.

A more complete examination of the relationships of zoropsids will be presented with our pending revision of the group in Australia.

Uliodon L. Koch 1873

Uliodon L. Koch 1873: 431, type species *Uliodon albopunctatus* L. Koch 1873 by subsequent designation of Simon 1892: 113.

Diagnosis.—Two claws but no true tufts. Leg scopula dense on tarsi of males and females. Males: cymbium with dorsal scopula; tibial apophysis in dorsal region of tibia; tegulum massive and extending over base of tibia; interlocking lobes with subtegulum subtle, if present; median apophysis an unsclerotized vane. Females: epigynal plugs present; PMS with line of spigots on dorsal surface.

Species Included.—*Uliodon albopunctatus* L. Koch 1873, *Uliodon cervinus* L. Koch, 1873, *Zora frenatus* L. Koch 1873.

Distribution.—Known only from New Zealand.

Remarks.—*Uliodon* differs from the Australian *Huntia* in the complete absence of a third claw, the presence of dense leg scopula and males have a much smaller tegulum and a small unsclerotized median apophysis. The epigyne figured by Koch's artist faithfully rended the epigynal plug and hence partially obscured the detail of the epigyne.

Forster had consistently considered species here placed in *Uliodon* as *Miturga* (e.g. Forster & Forster 1999). However, he had begun a revision of that group in New Zealand with RJR. As with many spider taxa in New Zealand, the Zoropsidae are very diverse and may constitute several genera. Hence, the above diagnosis is based upon males and females from the Auckland region and presently considered conspecific with *U. albopunctatus*.

Family Miturgidae Simon 1885

Diagnosis.—Differs from Zoridae in males having tibial apophysis with an unsclerotized zone and from the Ctenidae and Zoropsidae in lacking strong paired spines on tibiae and metatarsi I, II.

Two claws, true claw tufts present or scopula extending around claws; weak paired spines ventrally on tibiae and metatarsi I & II, basally divided median apophysis, RTA with unsclerotized zone and maxillae rounded rectanguloid with short diagonal groove. Retrocoxal hymen distinct on I. Eight similarly-sized eyes in two rows; from above, front row straight to slightly recurved, back row slightly procurved, straight to clearly recurved; tapetum grate-shaped. Females with spigots only apical on PMS.

Included genera.—Australian region; *Miturga*, *Diaprograpta* Simon 1909, *Zealoctenus* Forster & Wilton 1973. Middle East; *Prochora* Simon 1885. North & South America; *Teminius* Keyserling 1887.

Remarks.—Australian species currently placed in the otherwise Neotropical genus *Odo* Keyserling 1887 are all clearly considered miturgids but are not correctly placed in *Odo*.

The Eutichurinae lack the grate-shaped tapetum, critical for their inclusion in the Lycosoidea (Griswold 1993) and, unlike the lycosoids, have maxillae modified with an ectal constriction as in Clubionidae. The character used to align the Eutichurinae and Miturgidae was the elongate apical article of the PLS (Ramírez, Bonaldo, & Brescovit 1997) which is simply a synapomorphy of the genus *Miturga*. Hence, Deeleman-Reinhold's (2001) restora-

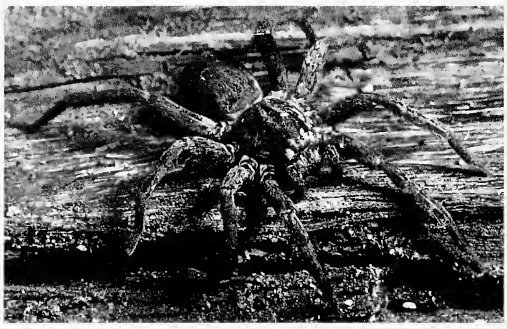


Figure 1.—*Mituliodon tarantulinus* (L. Koch), habitus.

tion of the Eutichurinae to the Clubionidae is upheld (contra Platnick 2001).

Subfamily Miturginae Simon 1885
Mituliodon new genus

Type species.—*Zora tarantulina* L. Koch 1873.

Diagnosis.—Differs from *Diaprograpta* and *Zealoctenus* in the extensive conductor in males and the form of the epigyne in females and from all other described Australian miturgid genera in the presence of true claw tufts. As more miturgids are described, the flattened form of the cymbium with retrolateral flare and the very extensive conductor will provide further distinguishing characters.

Description.—*Color:* Carapace yellow brown with darker banding medially, around edges and along striae. Legs yellow brown without pattern; abdomen fawn brown with paired central dark spots; ventrally black field with line of white dots breaking into two bigger dots posteriorly; 2 large spots anteriorly and 2 in front of spinnerets.

Carapace low, with low broad caput; fovea long, straight; silver and brown hairs enhance pattern; 3 bands of silver hair between eyes of back row. Eyes: 8 in 2 rows, both rows gently recurved; front row eyes smaller than those of back row; ALE each just past inside edge of PLE; front row eyes set close, ca. 0.7–1.0 diameter apart; back row eyes ca. 1 diameter apart. ALE look to side. Tapetum grate-shaped. Chelicerae small; teeth formula: 2r, 3p. Sternum scalloped shield; setation: uniform cover of bristles and hair. Labium short. Maxillae with deeply narrowed base, almost diamond-shaped, converging to base and apex from midpoint; apex rounded. Legs: coxae with small distinct anterior process; large, distinct retrocoxal hymen on coxae I; trochanteral notches ca. 1.5 x wider than deep on IV, shallower on I; no feathery hairs. Spines: tibiae I & II v2.2.2 not strong or overlapping; metatarsi I, II v2 long basal; prolateral spines on tibia I, II; proventral spine on femora. Scopula: dense on tarsi I-IV and metatarsi I-III, weak on IV, also present as two lateral fringes in distal half of tibiae I, II. Trichobothrial base laminate, collariform; cuticle finely grooved. Claws: 4–5 teeth on long, similar, paired claws; unpaired claw absent. Dense, wide tufts distally fused and reach to lower edge of claws. Spinnerets: colulus, an hirsute triangle; ALS conical; PLS basal segment as long as ALS but more slender with triangular coniform apical segment; PMS much smaller than PLS; ALS with 2 major ampullate spigots; 8–10 pyriforms. Male palp: tibia with flange-like distal retrolateral tibial apophysis with diagonal ridge and soft tissue beside that and distal triangular flat process beyond; cymbium wide, flattened, basal and basolateral margins wide, apical cone short without ventral groove; long wide shallow groove from base almost to tip of cymbium along retrolateral edge; embolus small, gourd-shaped, retrobasally reflexing back basally to be long and filiform around back of tegulum along long conductor; median apophysis has slender soft junction with embolus and with small, apical, retrolateral hook; tegulum n-shaped, distal, flat with large grooved conductor sweeping up from near embolus base to near tip of median apophysis; subtegulum wide, transverse, basal; slight scopula and thick setae behind cymbial tip.

Etymology.—An arbitary combination of letters formed from *Miturga* and *Uliodon*; the gender is masculine.

Included species.—*Mituliodon tarantulinus* (L. Koch 1873).

Distribution.—As for species.

Relationships.—Among the known Miturgidae (excluding the Eutichurinae), *Mituliodon*, *Diaprograpta* and *Zealoctenus* are unusual in possessing true movable claw tufts which are on separate pads beside the claws. In *Miturga*, claw tufts are absent; the scopula simply extends beyond the tarsal tip. No other miturgids, however, have the very extensive conductor. *Mituliodon* shares with other miturgids the basally divided median apophysis

and an unsclerotized zone on the tibial apophysis. A revision of the Australian Miturgidae will deal more fully with the relationships.

From fresh material of *Zora marmorea* Hogg 1896 and comparison with the types (in AMS and the Museum of Victoria), we have established that the species is a miturgid but does not belong in *Mituliodon* or any described genera. It will be placed elsewhere in a pending revision.

Mituliodon tarantulinus (L. Koch 1873) new combination
(Figs. 1–11)

Zora tarantulina L. Koch 1873: 445; Simon 1897: 106.
Zora australiensis L. Koch 1873: 441. NEW SYNONYMY.
Zora torva L. Koch 1873: 444. NEW SYNONYMY.
Miturga maculata Hogg 1900: 109. NEW SYNONYMY.
Syspira rubicunda Hogg 1900: 108. NEW SYNONYMY.
Miturga velox Hickman 1930: 114. NEW SYNONYMY.

Types.—*Zora tarantulina:* ZMH: Museum Godeffroy no. 8190: holotype male, Port Mackay, Queensland, Australia.

Zora australiensis: ZMH: holotype, subadult female, Wollongong, New South Wales, Australia.

Zora torva: holotype, male premolt, "Australia", Thorell collection, in RMS, examined.

Miturga maculata: BMNH 1907.2.24.1–5 (including 1 juvenile of *Miturga gilva* L. Koch): 2 juvenile females, 3 females, 2 males, Mt Macedon, Victoria, Australia: intact male here designated as lectotype, remainder as paralectotypes.

Syspira rubicunda: BMNH 1907.2.24.11–12: holotype female, paratype male, "Cheniston", Mt Macedon, Victoria, Australia.

Miturga velox: holotype male, paratype female, Launceston, Tasmania, Australia, QVM 13: 7325 and 7324, examined.

Description.—*Female*: (QM S36672) Color and Pattern: Union Jack pattern on yellow brown carapace: U-shaped darker areas (of hair) radiating from fovea along each interstrial ridge; longitudinal bands of darker hairs on caput broken by sinuous streaks arising between each pair of PME–PLE and PME–PME; curved area of silver hairs from between lateral eyes around PLE. Abdomen fawn brown with black flecking laterally and in posterior half paired small dark flecking; ventrally with a black field; behind epigastric furrow two large white spots, lateral of those 4 in a diamond-pattern posterior of that a triangle of 3 white spots pointed centrally; legs orange brown without annulations, scopula makes distal half of metatarsi I and II and tarsi I, II darker; sternum and coxae orange brown; maxillae, labium and chelicerae dark red brown.

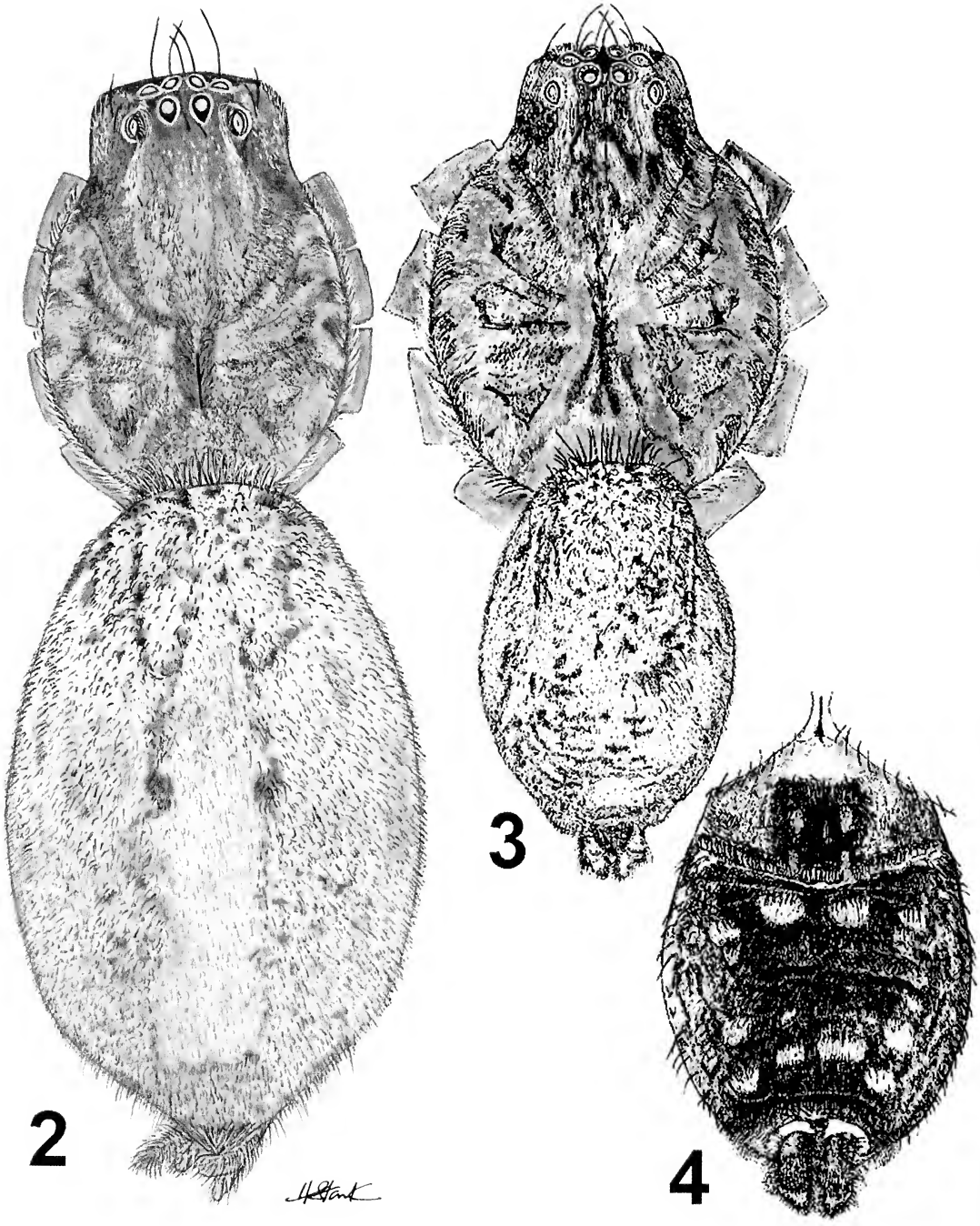
Carapace pear-shaped, rounded laterally with distinct but rounded cephalic portion; caput arched but gradually defined; fovea begins at end of caput and extends for last portion of thorax and slightly down posterior slope; light pilosity with cuticle evident in all parts; clypeus steep but short; chilum of 2 distinct triangles.

Eyes occupy 0.75 of head-width; front row recurved; from above AME set just out from cephalothorax margin; AME on mound look forward and to side; ALE on mound highest in front look to front and side; PME not on mound look up and to front; PLE on low mound look to side and up; all eyes of similar size, AME further from ALE than AME; likewise PME and PLE. Back eye row recurved and almost an eye diameter wide from front row. From in front, front row centers—straight with ALE (slightly larger) margins above and end below those of AME.

Chelicerae with low but distinct boss; fangs moderately long. Serrula a distinct curved line. Maxillae almost tear-shaped with 2 glabrous regions ventrally and proventrally near posterior apex; cylindrical in cross-section. Labium extends barely to half length of maxillae, broad. Sternum roundly cordate with elevated ridges opposite intercoxal spaces; no extension between any coxae.

Legs: coxae rounded, all of similar size with similar flange to *Miturga*. Trochanters all short, similarly (I–IV) and deeply notched. Relative lengths of leg segments: femur about equal to tibia longer than metatarsus much longer than tarsus = patella except IV, metatarsus longer than all. Pilosity: moderately long black bristles and fine hair not obscuring cuticle on legs; no evident clustering.

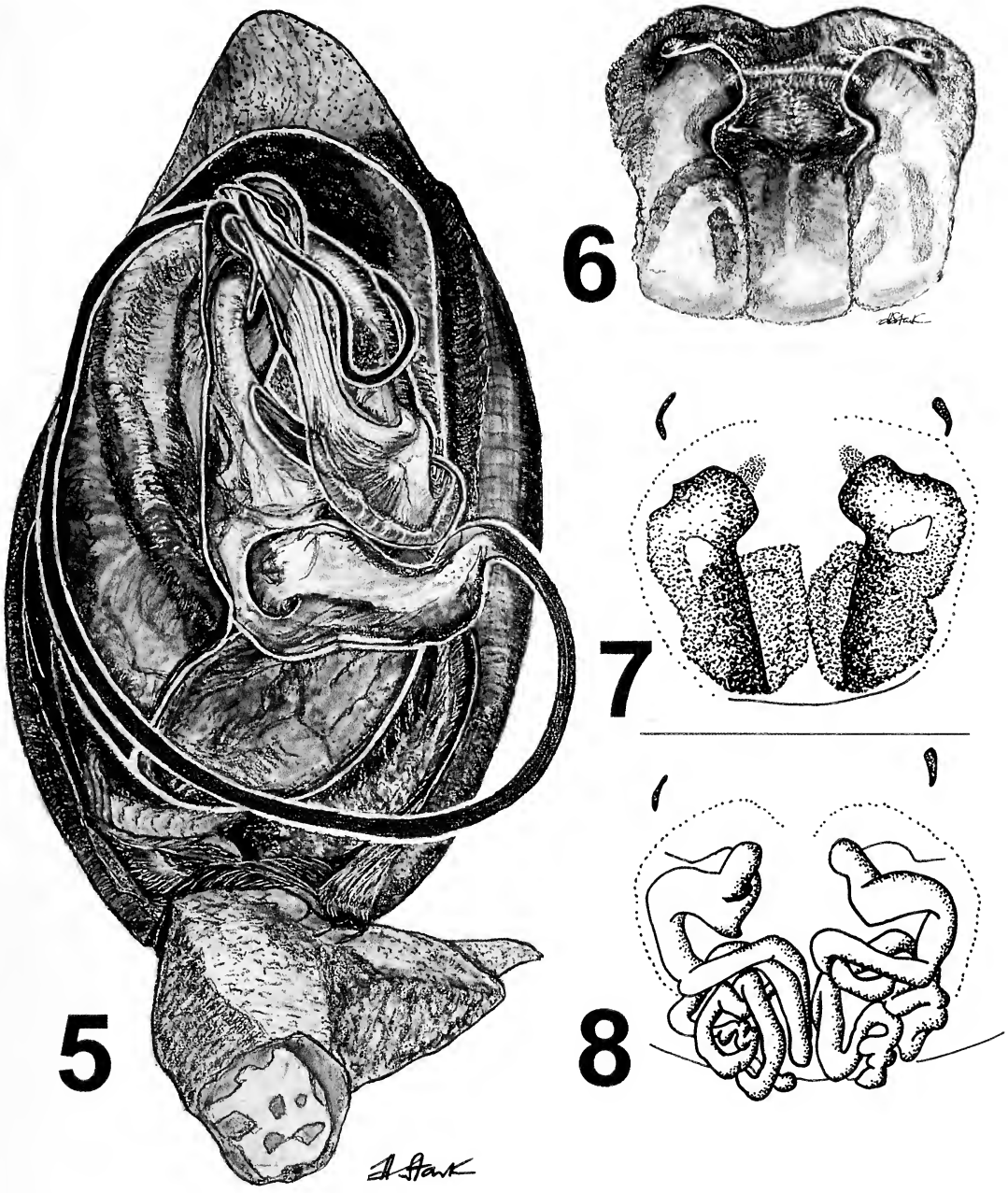
Scopula: dense, obscuring cuticle on metatarsi and tarsi I, II; laterally with scoop-like ridges of hair on tibiae I, II; thinner but entire and full tarsi and metatarsi III divided medially by setae on tarsi IV; 3 bands for 0.75 of metatarsi IV.



Figures 2–4.—*Mituliodon tarantulinus* (L. Koch). 2, female. 3, 4, male. 2, 3, cephalothorax and abdomen, dorsal view. 4, abdomen, ventral view.

Spines. I: fe p2d2r2w, pa 0, ti v2.2.2, me v2 long, basal. II: fe p4d2r2w, pa 0, ti v2.2.2, me v2 long, basal. III: fe p4d3r4, pa 0, ti p2d2r2v2.2.2, me p3r1v2 long, basal + 1 middistal. Palp: fe p1d4, pa p1, ti p3r2, ta p3r2.

Claws: palpal, long curved with 4–5 long teeth. Long paired claws with 3–5 teeth; tufts absent on female palp, small elsewhere, not as high as scopula and just covering teeth on claws; claws set well above tufts.



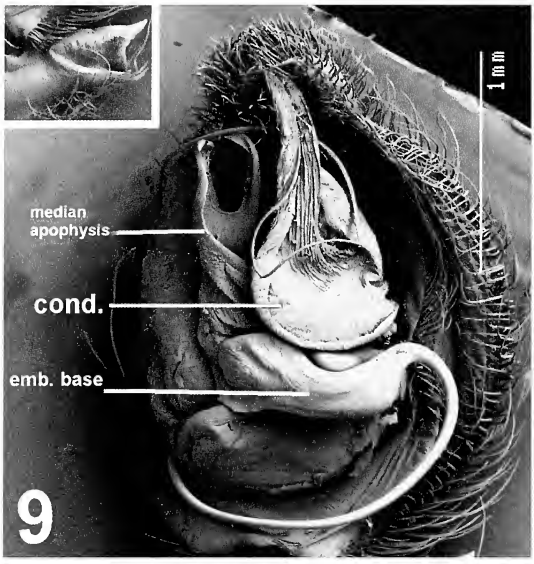
Figures 5–8.—*Mituliodon tarantulinus* (L. Koch). 5, male, tibia, cymbium & bulb, ventral left. 6, 7, epigyne. 8, vulva.

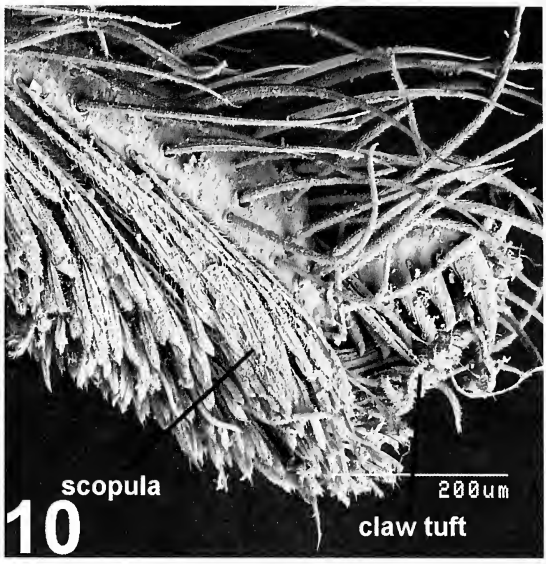
Trichobothria: 2 bands on each side dorsally of tibiae; trichobothria as long basally on tibia as distally; single line dorsally on tarsi with distal trichobothria longer.

Spinnerets: all of similar length but PLS smaller in diameter; PMS cylindrical; colulus a small setose area.

Epigyne: Two lateral lobes with inner anterior lobes plus medial ridge. Copulatory fossae lie behind anterior lobes; a large duct folds slowly and then reduces in diameter and forms complexly folded basal portion; fertilization ducts basal.

Male (QM S36201) (like female except as follows): Spines. I: fe p3d3r4, pa 0, ti p3d1r2v6, me v2 basal. II: fe p4d3r4, pa 0, ti





Figures 9, 10.—*Mituliodon tarantulinus* (L. Koch), male. 9, cymbium & bulb, ventral left, scanning electron micrograph with tibial apophysis (inset). 10, tarsus, lateral view showing different orientation of hairs in claw tufts and scopula.

p2r2v6, me v2 basal. III: fe p5d3r4, pa 0, ti p2d2r2v6, me p4r3v2 basal+ 1 distal. IV: fe p4d3r3, pa 0, ti p2d3r2v6, me p5r5v2.2.1.

Palp: As for genus.

Remarks.—As first revisers, the senior of the synonymous species in L. Koch (1873) is taken because the holotype is a male, the most distinctive of the sexes.

Variation.—Throughout its range *Mituliodon tarantulinus* is very consistent in sexual morphology with the biggest variation occurring in Western Australia where a subtle difference in the shape of the apical portion of the tibial apophysis is sometimes discernible. The pattern on the dorsal carapace is effectively a black Union Jack on a mottled brown background. The darkness of the background varies making the radiating lines less distinct in some specimens. The white pattern on the black field on the ventral abdomen varies from two convergent white lines to a series of dots. Neither of these variations shows any clear correlation with habitat, distribution or other morphology. However, around Adelaide, South Australia, the sternum of *Mituliodon tarantulinus* (where the two color forms are sympatric) is a deep burgundy red whereas elsewhere it is light to dark brown.

Distribution and Habitat.—*Mituliodon tarantulinus* is the most widely distributed species of the known Australian miturgids (Fig. 11). It is known from the Wet Tropics (Thornton Peak) in north Queensland, west to south central Queensland, and south along coastal and near coastal areas through New South Wales, Victoria, eastern Tasmania, southern South Australia and in the south-western corner of Western Australia. It has not been recorded from the Northern Territory. It is also known from Timor. The only common factor that may explain its distribution is the presence of a litter layer of some depth. Habitats with such a layer occur in rainforest, semi-evergreen vine thicket and eucalypt forests but not desert or grassland. The hypothesis needs further testing, however.

Biology.—*Mituliodon* is litter dwelling and nocturnally active. However, when a forest is subjected to vibration (at any time but diurnally most easily seen) from a slowly idling big engine (e.g. tractor or diesel 4x4) a number of spiders become very active (first reported by D. Hirst, XII International Congress of Arachnology, Brisbane 1992, Special Methods meeting). On a number of occasions, RJR has noted that larger *Mituliodon* can be seen running across the litter from over 20 m directly towards the vibration source.

Neither juveniles nor adults are taken commonly in vegetation sweeps nor are they often seen off the ground at night. Hence, any significance attributed to the presence of claw

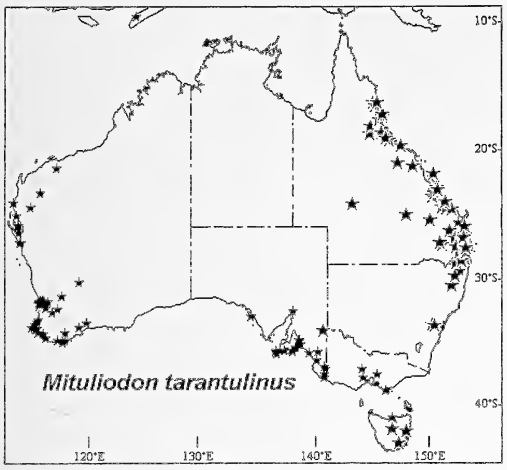


Figure 11.—Distribution map of *Mituliodon tarantulinus* (L. Koch).

tufts for scaling smooth vertical surfaces is without much support. Diurnally, *Mituliodon* is found under litter and when rotting logs resting on the ground are lifted or broken open. In Queensland, *Mituliodon* is often taken in houses.

The egg sac is a small soft disc attached to the underside of rocks and logs.

Toxinology.—Euphoria, dizziness, pain, and light-headedness have been reported after the bite (Queensland Museum records).

Material Examined.—TIMOR: WAM 99/1235:♀, Lelofui, site A, 9°32′S 124°14′E; WAM 99/1236: ♂, Gunung Mutus, summit, 9°31′S 124°16′E. WESTERN AUSTRALIA. WAM 93/1761:♀, Hovea, 31°53′00″S 116°06′00″E; WAM 98/429:♂, Barlee Range Nature Reserve, site BR 7, 23°22′45″S 115°52′50″E; WAM 99/1214–5: 2 ♂, Bush Bay, site BB 5, 25°07′54″S 113°46′05″E. Cape Cuvier, Quobba Station, site CU 6, 24°08′20″S 113°26′44″E: WAM 99/1216–7:♂ & ♀; WAM 99/1218–9: 2♂; WAM 99/1220–1: juvenile♀; WAM 99/1222:♂. WAM 99/1223:♂, Kennedy Range NP, site KE 1, 24°29′34″S 115°01′50″E. Nanga Station, site NA 3, 26°31′21″S 114°00′08″E: WAM 99/1224: ♂; WAM 99/1225: ♂; WAM 99/1226: ♀; WAM 99/1227: ♂. WAM 99/1228: ♂, Zuytdorp, site ZU 2, 27°16′00″S 114°02′00″E; WAM 99/1229: ♂, Zuytdorp, site ZU 4, 27°15′45″S 114°09′13″E. Zuytdorp, site ZU 5, 27°14′43″S 114°11′36″E, WAM 99/1230–1: 2 ♂; WAM 99/1232–3: 2 ♂. WAM 99/1234: ♂, Zuytdorp, site ZU 3, 27°15′50″S 114°04′14″E; WAM 99/1243: ♂, Ambergate Reserve, 33°42′S 115°20′E; WAM 99/1244: ♂, 14 km E. of Black Point, 34°25′30″S 115°41′30″E; WAM 99/1245: ♂, Capel, lot 7 NW Road, 33°33′S 115°33′E; Crowea, ridge site, 34°28′S 116°10′E: WAM 99/1248: ♀; WAM 99/1249–50: 2 ♀. WAM 99/1251: juvenile ♀, 3 km W. of Darradup, 34°05′S 115°34′E; WAM 99/1252: ♀, Dog Pool on Shannon River, 34°46′S 116°22′E; WAM 99/1253: ♂, Dryandra Woodland, 32°47′S 116°55′E; WAM 99/1254: ♂, Durokoppin Nature Reserve, site DKR F2, 31°30′S 117°44′E; WAM 99/1255–6: ♂, Faure Island, TL-31, 25°53′30″S 113°54′00″E; WAM 99/1257: ♀, Faure Island, TL-30, 25°53′30″S 113°54′45″E; WAM 99/1259: ♀, Gelorup Rise, Gelorup, 33°23′S 115°38′E; WAM 99/1260:♀, Gunjin Gully, 31°59′S 116°08′E; WAM 99/1261–2: ♂ 2J, Ledge Point, site 2, 35°01′S 118°00′E; WAM 99/1263:♂, Margaret River, 33°57′S 115°04′E; WAM 99/1264:♂, 17 miles NE of Millstream Stn homestead, 21°25′S 117°15′E. Mt Cooke, 32°25′S 116°18′E, WAM 99/1265: ♂, WAM 99/1266:♀, site 3; WAM 99/1267: ♀, site 3; WAM 99/1268:♀, site 3; WAM 99/1269–71: 2 ♂, 1♀, site 2; WAM 99/1272: ♂. WAM 99/1273:♂, Mt Observation, 31°54′S 116°33′E; WAM 99/1274:♂, Mt Jackson, site MJR 1, 30°24′45″S 119°14′45″E; WAM 99/1275:♂, 25 km SE of Mundaring, 32°04′S 116°21′E. Nedlands, 31°59′S 115°48′E: WAM 99/1276:♀; WAM 99/1277:♂; WAM 99/1278:♂; WAM 99/1279:♂; WAM 99/1280–1: 2♀; WAM 99/1282–3: 2♀; WAM 99/1284:♂; WAM 99/1285:♀; WAM 99/1286:♀; WAM 99/1287–8:♂, ♀; WAM 99/1289–90: ♀J; WAM 99/1291–2: 2♂; WAM 99/1293:♀; WAM 99/1294–5: ♂J; WAM 99/1296–7:♂, ♀; WAM 99/1298:♀; WAM 99/1299:♂; WAM 99/1300:♂; WAM 99/1301:♂; WAM 99/1302:♀; WAM 99/1303:♂; WAM 99/1304:♂; WAM 99/1305:♂. WAM 99/1306:♀, W. of South Australia/Western Australia border; WAM 99/1307:♀, Salter Point, 32°02′S 115°52′E; WAM 99/1308:♀, Stirling Range NP, SW spur of Mt Hasse, 34°23′S 118°04′E; WAM 99/1309–11: ♂ 2J, Torndirrup NP, Sharp Point, 35°07′S 117°52′E; WAM 99/1312: juvenile ♂, Tutanning [Nature Reserve], 32°32′S 117°20′E, T.Evans; WAM 99/1313: ♀, Wilson Inlet, site 2, 34°59′S 117°22′E; WAM 99/1314–6: ♂ 2J, Bold Park, site BP 1, 31°57′11″S 115°45′50″E; WAM 99/

1317–8: Bold Park, site BP 3, 31°56′30″S 115°46′27″E; WAM 99/1319: ♀, Bold Park, site BP 4, 31°56′29″S 115°46′01″E. WAM 99/1320: ♂, Dianella Open Space, sites DO 1, DO 2, 31°53′S 115°50′Es WAM 99/1321: ♂, Jandakot Airport, site JK 1, 32°05′36″S 115°52′39″E. *Kings Park.* WAM 99/1322: ♂, site 4/3, 31°58′15″S 115°50′05″E; WAM99/1323: ♀, site 5/2, 31°58′15″S 115°50′00″E; WAM 99/1324: ♀, site 4/8, 31°58′15″S 115°50′05″E; WAM 99/1325: ♀, site 4/3, 31°58′15″S 115°50′05″E; WAM 99/1326–7: ♂, ♀, 31°58′15″S 115°50′05″E, JD. *Perth Airport,* site PA 5, 31°58′03″S 115°58′11″E. WAM 99/1328–9: ♂ J, site PA 6, 31°58′05″S 115°58′05″E; WAM 99/1330: ♂, site PA 7, 31°58′34″S 115°58′25″E, JMW et al. WAM 99/1331–2: 1 ♂ 1J ♀, Talbot Road Reserve, site TR 2, 31°52′25″S 116°03′03″E; WAM 99/1333–6: 4 ♂, JD; WAM 99/1337: ♀; WAM 99/1338: ♀; WAM 99/1339: ♀, Tuart Hill, site TH 1, 31°52′49″S 115°51′30″E. WAM 99/1340–1: 2 ♀, Tuart Hill, site TH 3, 31°52′50″S 115°51′34″E. WAM 99/1342–3: ♀ J; WAM 99/1344: ♂, Woodman Point, site WO 2, 32°07′50″S 115°45′28″E; WAM 99/1345–6: 2 ♂, Woodman Point, site WO 1, 32°07′47″S 115°45′23″E; WAM 99/1246–7: 2 ♂, Cocanarup Timber Reserve, 33°38′S 119°54′E; WAM 99/1258: ♂, Fitzgerald River NP, 11 km NW. of Roes, 33°57′47″S 119°16′39″E; WAM 99/1354: ♂, Shenton Park Bush, site A, 31°57′52″S 115°47′57″E; WAM 99/1355–8: 4 ♂, University of W.A. Research Park, cnr Selby St/Und, 31°57′02″S 115°48′05″E; QMS32803: 1 ♂, Nedlands, 31°59′S 115°48′E; SAM N1999134: ♀, Sawyers Valley, 31°54′S 116°12′E. SOUTH AUSTRALIA. *Fleurieu Peninsula, Seg Fleurieu Survey.* SAM N1999123, 1999141: 2 ♀, 5km ENE Parawa, 35°32′27″S 138°24′24″E; SAM N1999122: ♂, 8km WSW Parawa, 35°34′25″S 138°16′18″E; SAM N1999135–6: 2 ♂, 7km E Mt Compass, 35°20′43″S 138°41′56″E; SAM N1999137–8: ♂, 11km E Mt Compass, 35°21′16″S 138°44′11″E; SAM N1999139: ♂, 6.75km NNE Mt Compass, 35°18′39″S 138°40′34″E; SAM N1999140: ♂, 7.5km WSW Parawa, 35°34′25″S 138°16′18″E. *Kangaroo Island.* SAM N1999114–5: 2 ♂, 0.4km W Rocky R NPWS HQ, 35°57′03″S 136°43′43″E; SAM N1999110: ♂, 1.6km NE Cape du Couedic Lighthouse, 36°02′45″S 136°42′55″E; SAM N1999118: ♂, 10km NW Parndana, 35°50′05″S 137°21′37″E; SAM N1999119: ♂, 4.7km WNW Gosse Oval, 35°47′30″S 136°55′30″E; SAM N1999120: ♂, 7.9km SW Cape Willoughby Lighthouse, 35°51′08″S 138°02′56″E; SAM N1999121: ♂, same data but 8.5km SW Cape Willoughby Lighthouse, 35°52′49″S 138°04′14″E; SAM N1999113: ♂, 7km N Ravine de Casoars, 35°47′S 136°37′E; SAM N1999112: ♀, Ravine de Casoars, 35°48′S 136°36′E; SAM N1999116: ♂, Rocky R crossing W ranger HQ., 35°57′S 136°43′E; SAM N1999117: ♀ + eggsac, Snake lagoon, Flinders Chase NP, 35°57′S 136°39′E; SAM N1999111: ♂, West Bay, 35°53′S 136°37′E. *Mt Lofty Ranges.* SAM N1999130: ♀, Belair, 35°00′S 138°38′E; SAM N1999128: ♂, Coromandel Valley, 35°02′S 138°38′E; SAM N1999127: ♂, same data; SAM N1999107: ♂ juv., Kyeema CP, 35°16′28″S 138°41′30″E; SAM N1999129: ♂, 1km S Coromandel Valley P.O., 35°02′S 138°38′E; SAM N1999124: ♀, Loftia Recreation Park, 35°02′S 138°42′E; SAM N1999125–6: 2 ♂, same data. SAM N1999100: ♂, Bottle-brush Nature Res., Caroline Forest, 37°58′S 140°51′E; SAM N1999131: ♂, Burnside, Adelaide (foothills), 34°56′S 138°38′E; SAM N1999106: ♂, Comaum, 37°14′S 140°56′E; SAM N1999105: ♂, Hoods Scrub, Joanna, 37°06′S 140°53′E; SAM N1999133: ♂, Wilmington, 32°39′S 138°06′E; SAM N1999109: ♂, 1.5km WNW Rabbit I. Dam, Mt Rescue CP, 35°55′22″S 140°19′19″E; SAM N1999103: ♀, 13km N Keilira Stn, 36°37′S 140°10′E; SAM N1999104: ♀, same data; SAM N1999108: ♂, 1km SW Stony Well, 35°58′22″S 139°31′44″E; SAM N1999132: ♂, Mitcham, Adelaide, 34°59′S 138°37′E; SAM N1999101–2:2 ♂, Mount Meridith, 15km N Mt Gambier, 37°40′47″S 140°53′08″E; WAM 99/1237–8: 2 ♀, Baird Bay, 33°09′S 134°22′E; QMS32005: 1 ♀, Renmark, 14k WNW, 34°06′S 140°36′E. VICTORIA. BMNH 1924.3.1.834: ♀, "Cheniston", Mt Macedon; WAM 99/1239: ♂, Coranderrk Reserve, Healesville, 37°41′S 145°31′E; WAM 99/1240–1: 2 ♀ 1J, Mirranahua Gap, Grampian Ranges; WAM 99/1242: ♀, 1 juvenile, 2 km N. of Porcupine Ridge, N. of Daylesford, 37°17′S 144°11′E; QMS34573: 1 ♂, Mt Macedon; SAM N199998: ♀, 1km NW Anakie Junction, Brisbane Ranges, 37°54′S 144°15′E; SAM N199999: ♀, The Gums, Wilsons Prom-

ontory, c. 38°55′S 146°15′E. QUEENSLAND. QMS32713: 1 ♀, Ashgrove, Brisbane, 27°27′S 153°02′E; QMS39538: 1 ♂, 2 ♀, Ayr, 19°34′S 147°27′E; QMS32692: 2 ♀, Bahrs Scrub, 27°45′S 153°10′E; QMS32705: 1 ♀, same data; QMS32700: 1 ♂, Bardon, Brisbane, 27°28′S 152°58′E; QMS32206: 1 ♂, Beerburrum, 26°57′S 152°58′E. *Beerwah Forestry Reserve,* 26°51′S 152°57′E, heath. QMS19569: 1 ♀; QMS32663: 2 juveniles; QMS32668: 1 ♀; QMS32676: 1 ♀; QMS32682: 1 juvenile. QMS27869: 4 juv., Bellenden Ker Ra, Centre Peak Summit, 17°15′S 145°50′E; QMS27870: 1 ♀, 1 juv., same data; QMS27861: same data; QMS27718: 1 ♂, Bellthorpe, 26°51′S 152°42′E, QMS39048: 1 ♂, Blackbutt Ra, base, 26°52′S 152°11′E; QMS32661: 1 ♀, Blackbutt Ra, summit, 5km E Benarkin, 26°52′S 152°11′E; QMS36814: 1 ♀, Boggomoss No 3, 25°26′S 150°00′E; QMS19689: 2 ♂, Bondoola (Stonier), 23°11′S 150°41′E; QMS32000: 1 ♀, Boyne R, H'way Xing, 23°55′S 151°19′E; QMS30691: 1 ♀, same data; QMS32715: 8 juv., Braemar SF, 27°12′S 150°50′E; QMS32741: 1 juv., same data; QMS30729: 1 ♂, Brisbane, Acacia Ridge, 27°28′S 153°02′E, spider bite; QMS32738: 1p juv., Brisbane, The Gap, 28°27′S 153°00′E, Brookfield, Gold Ck Reservoir, 27°29′S 152°55′E. QMS32697: 1 juv.; QMS32704: 1 ♀; QMS32698: 2 juv.; QMS32696: 1 juv.; QMS32703: 2 ♀. QMS32718: 20 juv., Bulburin SF, 24°29′S 151°35′E; QMS25608: 1 ♂, Bushley Stn, 23°31′S 150°14′E; QMS32675: 1 ♀, same data; QMS32689: 1 ♀, Calamvale, Brisbane, 27°37′S 153°02′E; QMS32733: 1 ♂, same data. CAMIRA, 27°37′S 152°55′E. QMS31001: 1 ♂; QMS29680: 1 ♀; QMS25525: 1 ♂; QMS23026: 1 ♀; QMS30596: 1 ♂; QMS30595: 1 ♂; QMS31351: 1 juv.; QMS32699: 1 ♂; QMS32736: 1 ♂; QMS32730: 1 ♂. QMS32742: 1 ♀, Capalaba, Brisbane, 27°31′S 153°11′E; QMS32727: 1 ♀, Carina Heights, Brisbane, 27°28′S 153°00′E; QMS32711: 1 ♀, Carina, Brisbane, 27°29′S 153°05′E; QMS32720: 2 juv., Crediton (7), 21°12′S 148°32′E; QMS25385: 1 ♂, Deepwater NP, 24°31′S 151°58′E; QMS21830: 1 ♀, Eight Mile Ck (NQ 31/2), 18°40′S 144°42′E; QMS22415: 1 ♀, 1 juv., Enoggera, Army Lands, 27°43′S 152°58′E; QMS7062: 1 ♀, Eungella (Schoolhouse), 21°07′S 148°28′E; QMS18856: 1 juv., Eungella NP, 21°11′S 148°30′E. EWAN MADDOCK DAM, 26°47′S 152°58′E. QMS32667: 1 ♀, (site B); QMS32664: 1 juv., (site E) ; QMS32665: 1 ♀, Old homesite (site F) ; QMS32673: 1 ♀, Site E, 26°47′S 152°58′E, heath; QMS32264: 1 juv., Site F; QMS32680: 1 ♀, Site C; QMS32257: 1 juv., Site C. QMS32716: 1 ♂, Forty Mile Scrub SW Mt Garnet, 18°04′S 144°50′E; QMS22154: 1 juv., Frenchville, 23°20′S 150°24′E; QMS4185: 1 ♀, Gatton, 27°34′S 152°16′E; QMS32726: 1 ♀, Goodna, Ipswich, 27°37′S 152°53′E; QMS32723: 1 ♀, Great Dividing Ra., near Teviot Brook; QMS32725: 1 ♂, 1 ♀, Griffith Univ., Brisbane, 27°28′S 153°00′E; QMS32719: 1 ♀, Jindalee, Brisbane, 27°31′S 152°55′E; QMS32684: 1 juv., Karawatha Forest, 27°37′S 153°05′E; QMS32677: 1 ♂, same data; QMS32695: 1juv., Kroombit Tops, 24°22′S 151°01′E. QMS39077: 1 ♀, Lake Broadwater, 27°20′S 151°05′E; QMS39526: 1 ♀, same data but Site 1; QMS39076: 1 ♂, 1 juv., same data but SW track; QMS32671: 1 ♂, Landsborough, 26°48′S 152°58′E; QMS32678: 1 ♀, same data; QMS32734: 8 juv., Malaan SF, 17°35′S 145°35′; QMS32672: 1 ♀, Meikleville Hill, Yeppoon, 23°05′S 150°42′E; QMS32674: 1 juv., same data; QMS32729: 1 ♂, Moreton I, S Eagers Swamp, 27°11′S 153°24′E; QMS32728: 1 ♂, Mt Coolum, 26°34′S 153°05′E, heathland; QMS32737: 3 juv., Mt Coot-tha, Brisbane, 27°29′S 152°57′E; QMS32683: 1 ♀, Mt Halifax, 19°06′S 146°22′E; QMS15981: 1 ♂, Mt Moffatt NP, Dargonelly Rock Holes, 25°01′S 147°57′E; QMS39049: 1 ♀, Mt Nebo, 1/2 way down track in Reserve, 27°23′S 152°47′E; QMS39285: 1 ♂, Mt Spurgeon (trap 4), 16°27′S 145°11′E; QMS22656: 1 ♂, Mt Windsor Tbld, Whypalla SF, 16°12′S 144°58′E; QMS33185: 1 ♀, same data; QMS25542: 1 ♀, N Tamborine, 27°54′S 153°08′E; QMS32670: 1 ♀, Nob Ck, 22°52′S 150°36′E; QMS32002: 1 ♀, North Bell Peak, Malbon Thompson Ra, 17°06′S 145°53′E; QMS39050: 1 ♀, North East I, Percy Is, 21°42′S 150°19′E; QMS32712: 1 ♀, North Stradbroke Is, Pt Lookout, 27°26′S 153°32′E; QMS32666: 1 ♀, Olsen's Caverns, 23°10′S 150°27′E; QMS14113: 1 ♀, Paluma Dam Rd, 18°56′S 146°08′E; QMS39075: 1 ♀, Ravenshoe, 17°36′S 145°28′E. *Rochedale SF,* 27°37′S 153°08′E. QMS32706: 1 ♂;

QMS32702: 3 juv.; QMS32688: 1 ♀; QMS32690: 1 juv.; QMS32708: 1 ♂; QMS32687: 1 ♂, under logs; QMS32707: 1 ♂, 1 juv.; QMS32709: 1 ♀; QMS32710: 1 ♂; QMS32691: 1 ♂, 2 juv.; QMS32693: 1 ♀. QMS19632: 1 ♀, Rockhampton, 23°21′S 150°32′E. *Roedean St, Fig Tree Pkt, Brisbane, 27°28′S 153°00′E, SE.Q.* QMS39051: 1 ♂; QMS32717: 1 ♂; QMS32735: 1 ♂; QMS39529: 1 ♀. QMS32681: 1 juv., Rosslyn Head (DW4), 23°10′S 150°47′E; QMS19587: 1 ♀, same data; QMS32722: 1 ♀, Samford, 27°23′S 152°50′E; QMS32679: 3 juv., South Percy I, Lagoon area, 21°45′S 150°17′E; QMS27561: 1 juv., same data; QMS27494: 2 ♂, same data; QMS27502: 1 ♂, same data. *Taroom District, Boggomoss.* QMS36210: 1 ♂, (No.19), 25°25′S 150°00′E; QMS36352: 1 ♂, 2 ♀, 1 juv., QMS36288: 1 ♂, 1 ♀, (No. 8), 25°27′S 150°02′E, baited flight trap; QMS36672: 1 ♀; QMS36201: 1 ♂, (No. 19), 25°25′S 150°00′E; QMS32724: 1 juv., Teewah Ck, Cooloola, 25°55′S 153°02′E; QMS32714: 2 juv., Teviot Brook, Boonah, 27°54′S 152°33′E; QMS32701: 1 ♀, Upper Kroombit Ck, Kroombit Tops, 24°25′S 151°02′E; QMS39528: 1 ♀, Valette Stn, in Ck Pd, 24°10′S 143°12′E; QMS32686: 1 ♀, Wallaman Falls, 18°36′S 145°47′E; QMS32790: 1 ♂, Wynnum West, Brisbane, 27°28′S 153°00′E; QMS32662: 1 ♂, 1 ♀, Yeppoon, Byfield Rd (DW18), 23°03′S 150°42′E; QMS32685: 1 ♂, Hidden Valley, Yeppoon, 20°56′S 147°11′E; QMS32731: 1 ♂, No locality data; QMS32669: 1 ♂, The Bluff, Keysland, 26°14′S 151°42′E. AMKS 6793: ♂ j, Bulburin SF (Nursery), 24°30′S 151°28′E; AMKS 9163: ♂, Thornton Peak, N of Daintree, 16°10′S 145°22′E; SAM N199995: ♂, Lookout, W of Glasshouse Mountains, c. 26.54′S, 152.57′E; SAM N199994: ♂, Munumburra Fauna Sanctuary, Mt Bauple, c. 25°47′S 152°34′E. NEW SOUTH WALES. AMKS 37440: ♂, London Bridge SF, 3.7km SW Lookout, 29°51′S 152°12′E; AMKS 37425: ♀, 0.5km from Wheatley Ck Rd on Camp Ck Rd, 28°46′S 152°19′E; AMKS 30395: ♂, Kanangra-Boyd NP, Boyd Plateau, 33°43′S 150°25′E; AMKS 7419: ♂, Richmond Ra SF, Jnct Wattle Ck Rd and Wattle Ck, 28°37′S 152°46′E; AMKS 36068: ♂, Richmond Ra SF, Wattle Ck Rd, 28°38′S 152°46′E; QMS39527: 1 ♂, Mt Victoria, 33°34′S 150°14′E; QMS32740: 1 ♀, Hillgrove, 30°34′S 151°53′E; SAM N199996: ♀, Clarence R, Copmanhurst, 29°35′S 152°46′E. TASMANIA. AMKS 30744: ♀ j, Great Lakes, 41°52′S 146°44′E; AMKS 34434: ♂, Ferntree, 42°54′S 147°16′E; AMKS 29025: ♀j, Eaglehawk Neck, 42°00′S 147°55′E; SAM N199997: ♀, George Town, 41°06′S 146°49′E.

Zealoctenus Forster & Wilton 1973

Zealoctenus Forster & Wilton 1973: 295. Type species *Zealoctenus cardronaensis* Forster & Wilton 1973 (holotype female in Otago Museum, Dundedin, examined) by original designation.

Diagnosis.—Eight similarly-sized eyes in two recurved rows, back row strongly recurved; ALE clearly closer to AME than PME or PLE; tapetum grate-shaped. Only 2 claws with true claw tufts. Scopula weak on leg I, strong on tibia to tarsi II, only on metatarsi and tarsi III, IV. Trochanters deeply notched. Two pairs of weak spines on tibiae and metatarsi I, II. Carapace and abdomen hirsute with longitudinal dark stripes. Female epigyne with medial ridge diverging anteriorly into two slightly diagonal ridges. Males unknown.

Included Species.—*Zealoctenus cardronaensis* Forster & Wilton 1973.

Distribution and Habitat.—Known only from Cardrona Valley, New Zealand, where Forster & Wilton (1973) reported them to be found in "grassland and scrub."

Remarks.—The female of *Zealoctenus* is virtually indistinguishable from those of the Australian miturgid *Diaprograpta* Simon 1909 which we are revising. The males of the latter have a very diagnostic palp and until males of *Zealoctenus* are known, we simply wish to note that the genera may prove to be synonymous but both are retained at present. The diagnostic feature of Ctenidae is putatively the close juxtaposition of the ALE with either the PME or PLE (see Raven et al. 2001) and that is not the case in *Zealoctenus*.

Family Zoridae F.O.P.-Cambridge 1893

Diagnosis.—Eight eyes in two recurved rows; from front, ALE at same level as AME or higher but clearly closer to AME than ALE. Claw tufts present or absent with no hairs around claws (*Hestimodema*); leg scopula weak or absent. Retrocoxal hymen distinct on I. Males without fracture on pedal tibia, without cymbial scopula, and without unscleroti-

zed region on tibial apophysis. C-shaped tegulum but basal to basolateral embolic origin for half circumference of bulb; single distal median apophysis; conductor short, membraneous. Females with spigots only apical on PMS. Strong and often long paired spines (2–7 pairs) on tibiae I, II, 2–3 pairs on metatarsi I, II.

Included genera (Australian region).—*Argoctenus* L. Koch 1878, *Odomasta* Simon 1909, *Hestimodema* Simon 1909, *Elassoctenus* Simon 1909, *Thasyraea* L. Koch 1878, *Simonus* Ritsema 1881.

Remarks.—Lehtinen (1967) placed *Elassoctenus* into the synonymy of the *Diallomus* Simon 1897 which he had transferred from the Ctenidae. Davies (pers. comm.) had examined the type species of both genera and found that, contrary to Lehtinen (1967), that *Elassoctenus* is a valid genus as it was listed (Davies 1985: 124). We also examined that material and concur on *Elassoctenus* and note that *Diallomus fuliginosus* Simon 1897 is a ctenid (from above and in front the ALE are beside the PME, the ctenid condition) whereas in *Elassoctenus harpax* Simon 1909 and other congeners the ALE are clearly below the PME from in front and lie anterior to them when viewed from above.

Argoctenus L. Koch 1878

Argoctenus L. Koch 1878: 990; Simon 1897: 123; Roewer 1954: 636; Davies 1985: 123. Type species *Argoctenus igneus* L. Koch 1878 (type specimen not located in ZMB, ZMH, BMNH, RMS or NHMW) by subsequent designation of Simon 1892: 132.

Aenigma Karsch 1878: 825: Bonnet 1955: 176. Type species *Aenigma australiana* Karsch 1878 (holotype female in ZMB, examined) by monotypy.

Aenigmaaranea Strand 1929: 11. Replacement name for *Aenigma* Karsch 1878 preoccupied in the Coleoptera (Newman 1836) Mollusca (Koch 1846) and Lepidoptera (Strecker 1876). First synonymized by Davies 1985: 123.

Aenigmaranea: Bonnet 1955: 176. Invalid emendation.

Miturgina Simon 1889: 244. Type species *Miturgina vittata* Simon 1889 (holotype juvenile female, in MNHP, examined). First synonymized by Simon 1897: 132.

Horioctenoides Main 1954: 42; Forster & Wilton 1973: 293; Davies 1985: 124. Type species *Horioctenoides bidentatatus* Main 1954 (holotype subadult female in WAM, examined) by monotypy. NEW SYNONYMY.

Nemoctenus Forster & Wilton 1973: 290. Type species *Argoctenus aureus* Hogg 1911 (holotype female in BMNH, examined) by original designation. NEW SYNONYMY.

Diagnosis.—Two claws and true claw tufts. Eyes of front row clearly smaller than those of back row; from above and in front, front row clearly recurved; from above back row strongly recurved; ALE small, from front upper edges not higher than lower edges of PME. 3–7 pairs of strong spines ventrally on tibiae I, II. Retrocoxal hymen present; pretarsal fracture absent; trochanters deeply notched. Strong paired spines on tibiae (2–7 pairs) and metatarsi (2 pairs) I, II. Scopula absent. Six spinnerets: ALS two segmented, coniform with domed tip; PLS with short domed apical segment. Male palp with RTA; cymbium often with retrolateral groove. Male palp with elongate RTA often with translucent vanes in three planes; cymbium boat-shaped, tapering to apical cone without dorsal scopula but most species with cluster of thick setae apically; cymbium commonly with deep retrolateral groove. C-shaped prolateral tegulum; median apophysis short, sinuous, base triangular narrows quickly, apex acuminate twisted, embolus long curved.

Distribution.—Australia, New Zealand and New Caledonia.

Remarks.—The type of *Horioctenoides bidentatus* is a subadult female and until adult material from the type locality is located its identity cannot be certain. However, only one large *Argoctenus* with the characteristic bell-shape on the abdomen is known from the region and it differs from the New Zealand *Argoctenus aureus* only in the lobes on the tibial apophysis.

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AFRARCHAEA GRIMALDII, A NEW SPECIES OF ARCHAEIDAE (ARANEAE) IN CRETACEOUS BURMESE AMBER

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ABSTRACT. *Afrarchaea grimaldii* new species (Archaeidae, Archaeinae) from 88–95 Ma (Cenomanian–Turonian) Upper Cretaceous amber (Burmite) from Myanmar (Burma) is described. This is the first spider to be described from this deposit and is the oldest known Archaeidae sensu stricto extending the known range of the family by approximately 50 Ma from the previously oldest recorded specimens in Baltic and Bitterfeld ambers, and provides further evidence that spiders were not severely affected by the end-Cretaceous mass extinction event. It represents the oldest fossil record of an araneophagic spider. This species could be used to argue for both the theory of mobilistic biogeography and ousted relicts to explain the zoogeography of the genus, but until new data become available, supports neither reliably.

Keywords: Myanmar, fossil spiders

Biological inclusions have been known from Burmese amber or Burmite for almost a century (Cockerell 1916), but hitherto no spiders have been described from this source (Ross & York 2000). Some of the spider families present in the Burmese amber collections in the Department of Palaeontology of the Natural History Museum, London, were listed in Penney (2000) and Rasnitsyn & Ross (2000); (the specimens listed under the families Eusparassidae and Myrmeciidae by the latter authors (which are probably misidentifications, pers. obs.) are no longer valid arachnological taxa and should read Sparassidae and Corinnidae respectively [e.g. Platnick 2002]). Grimaldi et al. (2002) listed eleven families provisionally recorded from Burmese amber, including the specimen described here. Zherikhin & Ross (2000) proposed a Late Cretaceous age for Burmite, and based on the shared insect taxa of this amber with other well-dated amber deposits it probably dates from the Cenomanian or Turonian (Grimaldi et al. 2002). Cretaceous amber spiders have previously been described from the Santonian of Siberia (Eskov & Wunderlich 1994), the Turonian of New Jersey (Penney 2002), the Barremian of the Isle of Wight (Selden, 2002) and the Upper Neocomian–basal Lower Aptian of Lebanon (Penney & Selden 2002).

The Archaeidae are small to medium-sized haplogyne, ecribellate araneomorph spiders which are distinguished from other spiders by the combination of promarginal cheliceral peg teeth and an abdomen–petiole stridulatory system (Forster & Platnick 1984). In addition, the three Recent genera: *Afrarchaea* Forster & Platnick 1984, *Austrarchaea* Forster & Platnick 1984 and *Archaea* Koch & Berendt 1854, have their carapace with the pars cephalica elevated above the pars thoracica, often constricted between the head (which bears long, slender chelicerae with a short fang) and thorax to form a distinct neck (Forster & Platnick 1984). Here, the first Cretaceous Archaeidae sensu stricto is described, from Burmese amber, and the systematics and biogeography of the family are briefly discussed. A checklist of fossil Archaeidae sensu lato is provided.

METHODS

Preservation.—Both specimens are preserved in Burmese amber or Burmite (for details of locality and stratigraphy, see Zherikhin & Ross 2000; Grimaldi et al. 2002) and belong to the Department of Entomology at the American Museum of Natural History (AMNH). The holotype, AMNH Bu–256 is preserved in a small piece (3 × 4 × 5 mm) of clear yellow amber suffused with darker bands, which represent layering of the resin at the time of exudation from the tree. This conclusion is supported because only one region, between two of these darker bands, contains

air bubbles. The spider is preserved in a layer without air bubbles; there are no syninclusions. There is some fracture damage as a result of specimen preparation however, overall this is an exquisitely preserved specimen.

Methods.—Prior to being received by the author the amber had been set in a clear plastic resin and cut and polished to reveal the inclusion. Further preparation was carried out at the AMNH as specified by the author to reveal further important taxonomic features. All measurements were made using an ocular graticule and are in mm. Drawings were done under incident light with camera lucidas attached to an Olympus SZH stereomicroscope and a Nikon Optiphot stereo compound microscope, and photographs were taken with a Nikon D1X digital camera attached to the Nikon microscope, using a 2.5× photoeyepiece and a 2× objective lens then manipulated in Adobe Photoshop.

Recent material examined.—*Afrarchaea ngomensis* Lotz 1996; 1 ♂, 1 ♀ from Ngome State Forest, KwaZulu/Natal Province; NCA 93/612 (coll. M. van der Merwe, Jan. 1993).

Abbreviations used in the text and figures.—In the leg formula (e.g. 1423), the legs are ranked in order of length (longest first). Tm is the ratio of the distance that a trichobothrium is located from the base of the metatarsus (e.g. Tm = 0.8 indicates that the trichobothrium is located eight-tenths of the way along the metatarsus, from the proximal end of the segment). Abbreviations used in the text and figures are as follows: ALE = anterior lateral eye(s); AME = anterior median eye(s); b = bulb; bs = blunt setae; car = carapace; cf = clypeal foramen; cs = cheliceral seta; e = embolus; ebl = extension of bulb lip; f = furrow; F = flaw in amber; fe = femur; fg = fang; LC = left chelicera; lot = lateral ocular tubercle; mt = metatarsus; mx = maxilla; op = opisthosoma; pa = patella; PLE = posterior lateral eye(s); PME = posterior median eye(s); Pp, = pedipalp; pt = peg teeth; RC = right chelicera; sp = spinneret region; T = trichobothrium; ta = tarsus; TA = tegular apophysis; ti = tibia; 1–4 = walking legs 1–4.

Repository abbreviations.—AMNH = American Museum of Natural History; AP = Amber Museum of Palanga, Lithuania; MCZ = Museum of Comparative Zoology, Harvard; MfN = Museum für Naturkunde Institut für Paläontologie, Humboldt-Universität zu Berlin; NCA = National Collection of Arachnida, Plant Protection Research Institute, Pretoria; PIN = Palaeontological Institute of the USSR Academy of Sciences, Moscow; SGPIH = Geologisch-Paläontologisches Institut und Museum, Hamburg.

SYSTEMATIC PALEONTOLOGY

Family Archaeidae Koch & Berendt 1854

Subfamily Archaeinae Koch & Berendt 1854

Afrarchaea Forster & Platnick 1984

Type species.—*Archaea godfreyi* Hewitt 1919 by original designation.

Distribution.—Recent species in South Africa and Madagascar, fossil species in Burmese amber, Myanmar (Burma).

Remarks.—*Afrarchaea* was erected as a monotypic genus by Forster & Platnick (1984) for *Archaea godfreyi* from South Africa and Madagascar. It was distinguished from the other genera by having a less constricted carapace "neck" and on the basis of the female genitalia. Eskov (1992) considered *Afrarchaea* a junior synonym of *Archaea*; however, this was not based on the examination of Recent specimens and has not been accepted by subsequent workers (Platnick 2002). Lotz (1996) described five new *Afrarchaea* species from South Africa and provided new data for *A. godfreyi*.

Afrarchaea grimaldii new species

Figs. 1–5

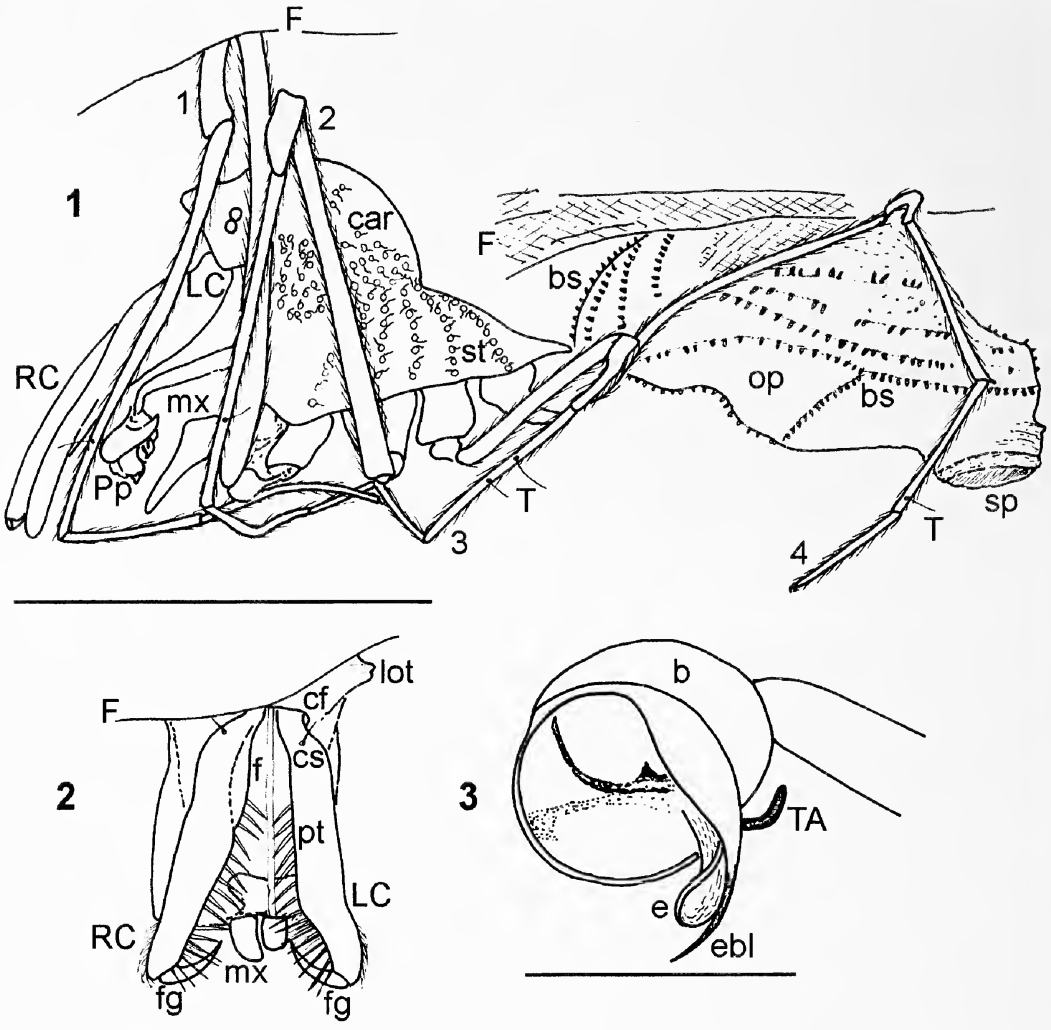
Archaeidae: Grimaldi et al. 2002: 28, fig. 18c.

Material examined.—Holotype: AMNH Bu–256, adult male, Burmese amber, Kachin: Tanai Village (on Ledo Road 105 km NW of Myitkyna); coll. Leeward Capitol Corporation 2000. Non-types: AMNH Bu–706, degraded specimen, same horizon and locality.

Diagnosis.—*Afrarchaea grimaldii* can be distinguished from all other species by having a bent tegular apophysis and a spoon-shaped embolus.

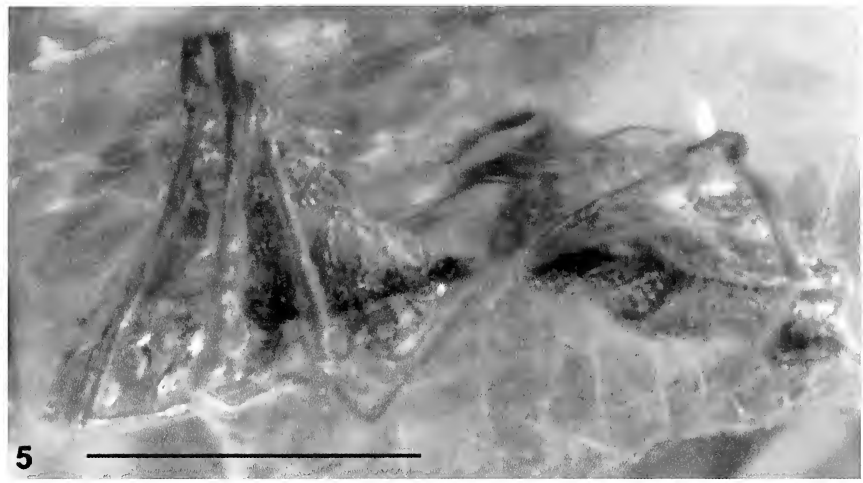
Etymology.—The specific epithet is a patronym in honor of Dr. David Grimaldi (AMNH) for his contributions to the study of amber and for loaning and assisting in the preparation of this material.

Description of holotype.—Body length 1.97; carapace 0.86 long, 0.43 wide, 0.64 high in region of pars cephalica; region between caput and thorax strongly developed and little differentiated from head; indent at junction



Figures 1–3.—*Afrarchaea grimaldii* new species. Holotype, AMNH Bu–256, Burmese Amber. 1, lateral view of whole specimen. 2, anterior view of chelicerae. Scale line 1.0 mm for both figures. 3, ventral view of pedipalp. Scale line 0.1 mm.

with pars thoracica 0.29 high, 0.46 long; with numerous distinct tubercles, each bearing a single seta lying flat against the carapace (Figs. 1, 5); narrow furrow running down midline from cheliceral foramen, visible when viewed anteriorly through the chelicerae (Fig. 2). ALE and PLE of equal size and contiguous, on a tubercle (Fig. 2), AME larger, PME not visible but presumably smallest as in Recent species (e.g. Lotz 1996). Clypeus slightly greater than diameter of AME. Chelicerae 0.79 long, slightly divergent and project out from the body at approximately 45 degrees when viewed laterally (Figs. 1, 5), strongly constricted basally where they insert into cheliceral foramen, thickened in proximal half when viewed laterally and tapering slightly at their tips along fang furrow, lacking triangular projections on apical promargin; each has a single erect dorsal seta close to proximal constriction; lacking cheliceral dentition, but numerous peg-teeth along promargin and long strong hairs along promargin in fang region (Figs. 2, 4); lateral stridulatory ridges not visible but presumed to be present; fang short and curved backwards. Sternum 0.50 long, 0.16 wide, possibly tuberculate, lateral margins appear to project slightly between coxae. Labium longer than broad, maxillae considerably longer than broad, slightly convergent,



Figures 4–5.—*Afrarchaea grimaldii* new species. Holotype, AMNH Bu–256, Burmese Amber. 4, anterior view of chelicerae. 5, lateral view of whole specimen. Scale line 1.0 mm for both figures.

projecting from body at similar angle to chelicerae (Fig. 1). Opisthosoma 1.11 long, height and width uncertain, wrinkled surface (Figs. 1, 5), presumably a taphonomic artifact resulting from dehydration process associated with amber preservation, presumably subglobular in life; no dorsal scutum. Opisthosoma covered with small patches of chitinous tissue each of which bears short, fat, blunt seta; spinnerets and anal tubercle not clear and surrounded by chitinous ring (Figs. 1, 5).

Leg formula 1423; leg 1 fe 1.14, pa 0.29, ti 1.00, mt 0.49, ta 0.34, total 3.26; leg 2 fe 0.86, pa 0.19, ti 0.74, mt 0.36, ta 0.29, total 2.44; leg 3 fe 0.57, pa 0.19, ti 0.40, mt 0.29, ta 0.24, total 1.69; leg 4 fe 0.93, pa 0.19, ti 0.71, mt 0.40, ta 0.31, total 2.64. All leg segments without spines, but with pubescence of fine setae; each metatarsus with single trichobothrium (Tm 1–4 = 0.8–0.9); tibiae 1–3 with at least one dorsal trichobothrium, none visible on ti 4 (Fig. 1). Some leg segments show evidence of annulations and darker markings, particularly in distal region; three tarsal claws on onychium: paired claws toothed, unpaired claw simple. Pedipalp has relatively long femur, large rounded bulb, bent tegular apophysis and spoon-shaped embolus (Fig. 3).

Female.—Unknown.

Distribution and age.—Burmese amber, Myanmar (Burma); probably Upper Cretaceous (see Zherikhin & Ross 2000): Cenomanian–Turonian (see Grimaldi et al. 2002)

Remarks.—This specimen conforms with the diagnostic characters of the genus given by Forster & Platnick (1984). It can be excluded from the remaining archaeid genera as follows: *Archaea* C.L. Koch & Berendt 1854, because it lacks the distinctive slender neck between the head region and the pars cephalica; *Baltarchaea* Eskov 1992, because it lacks the cephalic posterior angular projections, the abdomen does not extend beyond the spinnerets and the legs and chelicerae are not comparatively short; *Mimetarchaea* Eskov 1992, because it lacks the mimetid-like metatarsal spines on legs 1 and 2; *Austrarchaea* Forster & Platnick 1984, because the neck in the fossil specimen is too short, as is the embolus of the male palp; *Jurarchaea* Eskov 1987, because although Eskov (1987) was somewhat ambiguous with his diagnosis, in that he did not provide any distinct autapomorphies for his new taxa, but provided a list of general morphological descriptions that he later emphasized may be somewhat speculative, he placed this genus closer to the families Pararchaeidae and Holarchaeidae than Archaeidae sensu stricto. There are no spine-like horns sensu Lotz (1996) visible on pars cephalica of the fossil, but these are small in Recent specimens and may be present in the fossil but obscured by the legs or flaws in the amber. Specimen Bu–706 is preserved in a clear piece of amber with a spider syninclusion (possibly Oonopidae). It is severely degraded, barely visible, and it is only with a reasonable degree of imagination that the

raised pars cephalica and elongated chelicerae can be seen. For this reason it is very tentatively assigned to this species. Ecological observations of Recent archaeids are sparse, but all evidence suggests that they are araneophagic, free-moving, cryptozoic hunters (Forster & Platnick 1984). Most *Afrarchaea* in collections have been caught using pitfall traps or through sifting leaf litter (Lotz 1996). There is no evidence to suggest that the closely related families Holarchaeidae, Pararchaeidae and Mecysmaucheniidae are also araneophagous (Forster & Platnick 1984). Using the premise of behavioral fixity, which states that fossil organisms can be expected to have behaved in a similar manner to their Recent relatives at genus and often at family level, the specimen described above represents the oldest known occurrence of araneophagy in the spider fossil record (*Jurarchaea* belongs either in the family Pararchaeidae or Holarchaeidae [see Eskov 1987]). This is the first occurrence of *Afrarchaea* in the fossil record, taking the genus back 88–95 Ma, and is also the oldest record of the Archaeidae sensu stricto, extending the known range of this family by approximately 50 Ma from the previous oldest records in Baltic and Bitterfeld ambers. These fossils extend the known range of yet another Recent spider family through and beyond the end Cretaceous mass extinction event, suggesting that this catastrophe had little effect on the araneofauna, and provides further evidence for the great longevity for many Recent spider families (Selden & Penney 2001) and genera (e.g. Penney 2002).

DISCUSSION

The spider family Archaeidae is unique in that it was first described from three fossil species in Baltic amber (Koch & Berendt 1854) in a paper published posthumously by Menge (1854) who added three more new species. The first Recent species was discovered in Madagascar a quarter of a century later (O. Pickard-Cambridge 1881) and subsequently they have been found in Africa and other regions of the southern hemisphere (e.g. Harvey 2002). It is also, to my knowledge, the only family to have received paleontological treatment by that most eminent of arachnologists, Eugène Simon, who described a new species preserved in Baltic amber (Simon 1884). The specimens described by Koch & Berendt (1854) and Menge (1854) were considered lost for many years (e.g. Forster & Platnick 1984), however, many of Koch & Berendt's (1854) types are kept in the Institut für Paläontologie, Museum für Naturkunde, Zentralinstitut der Humboldt-Universität zu Berlin but those of Menge are still considered lost (Table 1).

The taxonomic composition and systematic placement of the Archaeidae sensu lato continues to stimulate lively debate. Since its original description, ten Recent (two with fossil representatives) and four strictly fossil genera have at one time or another, been placed within the Archaeidae; these are now distributed among the six families: Archaeidae sensu stricto, Holarchaeidae, Mecysmaucheniidae, Pararchaeidae, Tetragnathidae and Salticidae (e.g. Eskov 1992; Platnick 2002). As currently delimited, Archaeidae sensu stricto contains 18 Recent species in three genera (Platnick 2002; Harvey 2002) and ten fossil species (Archaeidae sensu lato) in five genera (Table 1). Holl (1829) described the new genus and species *Entomocephalus formicoides* from Baltic amber. This was listed as belonging in the Archaeidae by Petrunkevitch (1958) and to my knowledge this is the only mention of this taxon in the literature since its description. Holl's figure of this specimen (plate 8: fig. 68a) is almost certainly a salticid probably belonging to the genus *Myrmarachne* MacLeay 1839, even though the figure and description have the specimen with only six eyes. If indeed this is the case, then under the ICZN law of priority, *Entomocephalus* Holl 1829, precedes *Myrmarachne* MacLeay 1839. However, the location of the specimen on which the description was based is unknown, and the description of the genus consisted of only one sentence. The name *Myrmarachne* is well established, in common usage and should probably be maintained unless Holl's fossil specimen can be located. *Eoarchaea* Forster & Platnick 1984 was erected based on a single immature amber spider (Forster & Platnick 1984). No mature specimens of this species are known and the fossils attributed to it probably belong to various other *Archaea* species (Eskov 1992).

Archaeidae was divided into four families: Archaeidae sensu stricto, Mecysmaucheniidae, Holarchaeidae and Pararchaeidae by Forster & Platnick (1984) in a review of the su-

Table 1.—Described fossil Archaeidae sensu lato (standard typeface = synonym). * = type species; † = fossil taxon; ? = dubious taxon; ‡ = the type specimens of Koch & Berendt (1854) were considered lost for many years but many are kept in MfN (Pietrzeniuk pers. comm. 1995), however, this specimen was not found in their collections (Neumann pers. comm. 2002); § the type specimens of Menge (1854) are currently considered lost. His collection was originally donated to the Westpreussische Provinzialmuseum, Gdańsk (formerly Danzig), which was established in 1880. In 1945 the collection was moved to a number of villages in northern Poland and has not been seen since. Although single samples of his collection have been found in Germany and Poland, there seems little hope that further items will be found (Koteja pers. comm. 2002; see Kosmowska-Ceranowicz [2001]).

Species	Type data	Distribution	Remarks
Afrarchaea grimaldii new species	AMNH Bu-256	Burmese amber	
Archaea copalensis Lourenço 2000	SGPIH Type.Kat.Nr. 4351	Madagascan copal	Sub-fossil
Archaea hyperoptica Menge 1854 *Eoarchaea hyperoptica*: Forster & Platnick 1984	Type lost§	Baltic + Bitterfeld ambers	MCZ No. 7148 (129) designated as neotype (Petrunkevitch 1950)
Archaea incompta Menge 1854	Type lost§	Baltic amber	Considered a nomen nudum (Bonnet 1955)
Archaea levigata Koch & Berendt 1854	MfN MB.A 1083	Baltic amber	
Archaea paradoxa Koch & Berendt 1854* *A. sphinx* Menge 1854§: Eskov 1992	Type lost‡	Baltic amber	Non-type material: male, AP 4092. Type species designation by Thorell (1870)
Archaea pougneti Simon 1884	Type female lost	Baltic amber	Two non-type males AP 14902, AP 6334 (o-Eo 17781/AP 6334)
Baltarchaea conica (Koch & Berendt 1854)* *Archaea conica* Koch & Berendt 1854	Type lost‡	Baltic amber	Belongs to Mecysmaucheniidae (Eskov 1992)
Jurarchaea zherikhini Eskov 1987*	PIN 2339/2607	Upper Jurassic, Kazakhstan	Belongs in Pararchaeidae or Holarchaeidae (Eskov 1987)
Mimetarchaea gintaras Eskov 1992*	AP 19566	Baltic amber	Belongs in Pararchaeidae or Holarchaeidae (Eskov 1992)

perfamily Palpimanoidea. They also placed a number of disparate families (Mimetidae, Micropholcommatidae, Textricellidae) alongside the archaeoids, increasing the size of the Palpimanoidea considerably, which had previously consisted of only three families: Palpimanidae, Stenochilidae and Huttoniidae. However, few subsequent authors agreed with these authors' concept of the Palpimanoidea (see discussions in Eskov 1987, 1992; Coddington & Levi 1991), the monophyly of which was questioned. The superfamily Palpimanoidea was cut back to its original size by Schütt (2000), based on a reanalysis of the autapomorphies proposed by Forster & Platnick (1984). However, the correct systematic placement of the archaeids remains uncertain (Schütt 2000).

Fossils are often considered to be less useful than Recent specimens for systematic studies because of their imperfect preservation. However, they are of paramount importance in studies of historical biogeography, and can play a decisive part in the falsification of proposed hypotheses (e.g. Eskov 1990). For example, the current Gondwanan distribution of the Recent species of the spider family Archaeidae supports the theory of mobilistic biogeography i.e. that the fragmentation of Gondwanaland and the subsequent continental drift can explain their current distribution. However, because fossils of this family occur in Baltic amber (Koch & Berendt 1854) and from the Jurassic of Kazakhstan (Eskov 1987), the paleontological data contradict this hypothesis and a different explanation is required (the specimen reported from Dominican amber by Wunderlich [1999] is actually preserved in Madagascan copal [Wunderlich, pers. comm. 2000]). The theory of ousted relicts (e.g. Eskov & Golovatch 1986) proposes that austral disjunctions result from a formerly pancontinental distribution followed by the extinction of 'intermediate links' from the northern continents. There is a considerable amount of paleontological data, in the form of northern hemisphere fossil representatives of Recent austral taxa, which tends to be the rule rather than the exception, in support of this theory (Eskov 1987). This newly described amber archaeid spider provides new paleontological evidence that could be used to support both the above hypotheses. After a short phase of intra-continental rifting the breakup of east and west Gondwanaland was initiated by seafloor spreading between Africa and Madagascar in the Somali basin during the Jurassic quiet interval (c. 165 Ma), with the landmass of Madagascar + India eventually separating from Africa during the late Jurassic (152 Ma) (McLoughlin 2001). Madagascar separated from the Seychelles–India block 95–84 Ma and India migrated rapidly north reaching equatorial latitudes by the Eocene and combining with southern Asia (including West Burma) only about 43 Ma (McLoughlin 2001). West Burma had separated from northeastern Gondwana in the late Triassic–late Jurassic during the formation of the Neotethys Ocean and was accreted to southeast Asia by the late Cretaceous (McLoughlin 2001). Therefore, the occurrence of this genus in Burmese amber could be used to support the theory of mobilistic biogeography for its Recent distribution only if it existed throughout Gondwanaland during the late Triassic–late Jurassic. Three spiders have been described from the Triassic (Selden & Gall 1992; Selden et al. 1999) but none were placed in Recent genera. The currently more plausible explanation for the presence of *Afrarchaea* in this locality is that it is an ousted relict from a formerly pancontinental distribution in northern paleolattitudes as is the case for *Archaea*, another Recent archaeid genus, and presumably also the sister taxon of *Afrarchaea*.

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SHORT COMMUNICATION

SPIDER PREDATION: SPECIES-SPECIFIC IDENTIFICATION OF GUT CONTENTS BY POLYMERASE CHAIN REACTION

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ABSTRACT. We extend detection of arthropod predator gut contents by polymerase chain reaction (PCR), heretofore restricted to insect predators, to spiders. Single individuals of the corn lead aphid, *Rhopalosiphum maidis*, were detected in the guts of spiderlings of *Oxyopes salticus* up to 12 h after feeding; individuals of the congeneric bird cherry oat aphid, *R. padi*, were not detected. Unfed *O. salticus* and *Misumenops* sp. were also negative.

Keywords: Polymerase chain reaction, PCR, predation, gut analysis

Spiders tend to be small, cryptic feeders and, having extra-oral digestion and sucking mouthparts, exhibit amorphous gut contents; all of these attributes make it very difficult to obtain data on predation rates (Stuart & Greenstone 1990). Some information can be gathered by direct observation (Greenstone 1999), but gut analysis of field-collected spiders is the least disruptive and most efficient means to acquire data on predation (Stuart & Greenstone 1990).

The state-of-the-art for arthropod predator gut analysis has been serological assay. When monoclonal antibodies are used, specificity can be exquisite, extending to the species, stage, and even instar level (Greenstone & Morgan 1989; Symondson & Liddell 1993; Greenstone & Trowell 1994; Hagler et al. 1994; Ruberson & Greenstone 1998; Agustí et al. 1999a; Symondson et al. 1999; Harwood et al. 2001). Nevertheless, the production of monoclonal antibodies is an expensive and involved process comprising scores of steps with stochastic determinants of success (Greenstone 1996), and although monoclonal antibodies were described more than 25 years ago (Köhler & Milstein 1975), only a handful of arthropod ecologists have used them to study predation.

An appealing alternative is the detection of prey DNA in predator guts (Agustí et al. 1999b, 2000; Zaidi et al. 1999; Chen et al. 2000). The approach has several advantages: (1) the techniques necessary to develop molecular probes are widely known and in some cases have been subsumed into commercial kits; (2) a variety of candidate target regions have already been sequenced in insects, providing information on their variability and hence suitability as probes; (3) once prey species-specific primers have been designed and published, any investigator can have them manufactured cheaply and use them in reproducible protocols.

We have targeted the cytochrome oxidase II (COII) gene in our research on cereal aphid biocontrol. Being a mitochondrial gene, it occurs as multiple copies per cell, which increases the likelihood of successful amplification in gut extracts. It also exhibits various levels of variability (Zhang & Hewitt 1996), allowing closely related species to be separated. Finally, sequences are already available for several aphid species (Rouhbakhsh et al. 1996; Sunnucks & Hales 1996). Here we present the results of a pilot study designed to determine whether a the PCR assay demonstrated to detect cereal aphids species-specifically in insect predators (Chen et al. 2000) will also work in spiders.

Russian wheat aphids, *Diuraphis noxia* (Mordvilko), corn leaf aphids, *Rhopalosiphum maidis* (Fitch), and bird cherry-oat aphids, *R. padi* (L.), from colonies at the USDA-ARS Plant Science Research Laboratory in Stillwater, Oklahoma, were maintained at ≈25°C and a photoperiod of 12:12

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(light:dark) h on wheat. Second and third instars of the striped lynx, *Oxyopes salticus* Hentz 1845, and spiderlings of an unidentified species of *Misumenops* F.O.P.-Cambridge 1900, were collected by D-vac from wheat and alfalfa fields at the Oklahoma State University North Central Research Station in Chickasha, Oklahoma, on 29 November 2000. Voucher specimens have been deposited in the Cereal Genetics Research Library of the USDA-ARS Plant Science and Water Conservation Research Laboratory.

Spiders were starved for 1 d, placed in an incubator simulating field temperatures at mid-canopy level in a wheat field at the same locality in the spring of 1999 (Chen et al. 2000), and offered 3 *D. noxia*. Experimental spiders, all *O. salticus*, were then starved for an additional 3 d before being offered a single *R. maidis*, offered five additional *D. noxia* to simulate continued feeding, placed back into the incubator, and then killed by freezing at 4 h (four individuals) or 12 h (six individuals) post-feeding; those that did not consume the corn leaf aphid within 1 h were dropped from the experiment. Two control *O. salticus* were fed a single *R. padi* and killed after consuming it. Additional starved spiders, one of each species, were included as a check against false positives due to amplification of spider DNA. The first 4 d of this protocol were designed to ensure that DNA from any *R. maidis* ingested in the field would have been rendered undetectable before the spiders were killed.

We modified the methods of Zhu & Greenstone (1999) to extract total DNA. Insects or spiders were placed individually in 1.5-ml microcentrifuge tubes and homogenized using a battery-powered homogenizer (Midwest Scientific, St. Louis, MO) in 100 µl or 500 µl, for aphids and spiders, respectively, of isolation buffer (Chen et al. 2000). The homogenate was vortexed briefly and incubated for 30 min at 65°C. The solution was transferred to a new tube and extracted once with one volume of chloroform/isoamyl alcohol (24:1). One-tenth volume of 3.0 M sodium acetate and two volumes of ice-cold 100% EtOH were added to the tube. DNA was then pelleted by centrifugation, dried, and resuspended in 200 µl distilled water.

Protocols for the design of species-specific mitochondrial COII primers for six cereal aphid species have been given elsewhere (Chen et al. 2000). PCR reactions, using *R. maidis* primers ClaCOIIF and ClaCOIIR1 (Table 2 of Chen et al. 2000), were performed as described by Chen et al. (2000). PCR products were separated on a 1.5% agarose gel, stained with ethidium bromide, and photographed under UV light.

All *O. salticus* fed *R. maidis* were positive by PCR for 4 h and 12 h post-feeding. All unfed *O. salticus* and *Misumenops* sp., and *O. salticus* fed *R. padi*, were negative (Fig. 1). These negatives demonstrate either that the first 4 d of the experimental protocol were sufficient to render all *R. maidis* DNA in the guts of the experimental *O. salticus* undetectable, or that the animals had not consumed *R. maidis* in the field prior to capture.

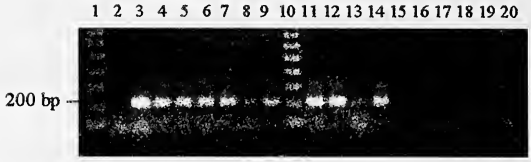

Figure 1.—PCR amplification of *Oxyopes salticus* fed *Rhopalosiphum maidis*. Lanes 1, 10 and 20: 100 bp DNA ladder. Lane 2: *R. padi* DNA. Lane 3: *R. maidis* DNA. Lanes 4–7: *O. salticus* fed *R. maidis* killed 4 h after feeding. Lanes 8–9 and 11–14: *O. salticus* fed *R. maidis* killed 12 h after feeding. Lane 15: Unfed *O. salticus*. Lane 16: Unfed *Misumenops* sp. Lanes 17 and 18: *O. salticus* fed *R. padi*. Lane 19: Negative control (no template).

This is the first report of spider gut analysis by PCR. By focusing on two aphid congeners, we have made a very stringent case for specificity. The assay will detect 10^{-7} aphid equivalent (Chen et al. 2000). If run in a microplate format, an individual PCR assay costs ≈$0.28; this compares favorably to the only technology with similar specificity and sensitivity, ELISA with monoclonal antibodies, at $0.21 (Chen et al. 2000).

Before assay data from field-collected animals can be used, the detectability half-life (Greenstone & Hunt 1993) for a single aphid must be determined. Detectability half-lives are necessary because mere determination of the proportion of predator individuals positive for prey DNA is not a reliable indicator of the relative importance of any given predator taxon. For example, the green lacewing *Chrysoperla plorabunda* has a half-life (3.95 h) for detectability of *R. maidis* DNA that is only 0.45 that (8.78 h) of the ladybird beetle *Hippodamia convergens* (Chen et al. 2000). Consequently, the consumption of a single *R. maidis* is 2.2 times as likely to be detected in an *H. convergens* individual as in a *C. plorabunda* individual; another way to look at it is that a positive *C. plorabunda* is "worth" 2.2 times as much as an *H. convergens* positive.

We may expect to find dramatic differences in detectability half-lives as more predator taxa are studied. For example, in the analogous case of detecting protein antigens in serological predator gut analysis, staphylinid beetles appear to have short detectability half-lives (Sunderland et al. 1987), and spiders much longer ones (Greenstone 1983; Ragsdale et al. 1981; Harwood et al. 2001). Whether such differences between spiders and other arthopod predators will also be found with respect to

DNA digestion will not be known until rigorous comparative studies employing very large sample sizes (cf. Chen et al. 2000) have been conducted.

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SHORT COMMUNICATION

COHABITATION BETWEEN AN ADULT MALE AND A SUBADULT FEMALE IN A BURROWING WOLF SPIDER (ARANEAE, LYCOSIDAE)

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ABSTRACT. We report a case of cohabitation between an adult male and a conspecific subadult female *Lycosa tarantula* (Linnaeus 1758) (Araneae, Lycosidae). Cohabitation was observed during a field study in a population near Madrid city (central Spain). The male was first observed in the female burrow four days before the female maturation molt. Both individuals remained together until female maturation occurred. Mating occurred two days after female maturation, at a much younger age than non-cohabiting females. The possible mechanisms by which adult males find subadult female burrows are discussed.

RESUMEN. Describimos un caso de cohabitación entre un macho adulto y una hembra subadulta de *Lycosa tarantula* (Linnaeus 1758) (Araneae, Lycosidae). Observamos la cohabitación durante un estudio de campo realizado cerca de la ciudad de Madrid, en el centro de España. Encontramos por primera vez al macho en el interior del nido de la hembra cuatro días antes de la maduración de ésta. Los dos animales permanecieron en el nido todo ese tiempo, y se aparearon dos días después de la muda de maduración de la hembra. Esto ocurrió a una edad muy inferior a la de las hembras que no cohabitaron con ningún macho. Discutimos los posibles mecanismos por los que los machos adultos encuentran los nidos de las hembras subadultas.

Keywords: Sexual cohabitation, Lycosidae, *Lycosa*

Sexual cohabitation, in the general sense of a male and a female dwelling together, is a relatively widespread phenomenon in spiders (Jackson 1986). It has been described in many families and genera, including araneids (Fahey & Elgar 1997), eresids (Schneider 1997), salticids (Jackson & Mcnab 1991; Jackson 1995), linyphiids (Suter & Walberer 1989; Suter & Sánchez 1991) and lycosids (Miller & Miller 1986, 1987).

Descriptions of sexual cohabitation are rather diverse and include situations in which adult males are found in the webs of adult females for more time than required for copulation (Suter & Walberger 1989; Suter & Sánchez 1991), and those in which adult males are found dwelling with subadult females (Miller & Miller 1986, 1987; Fahey & Elgar 1997; Schneider 1997). If there is first male sperm priority and the female reproductive status is difficult to assess, cohabitation between adult males and subadult females may be interpreted as a sort of pre-mating mate guarding. It would increase the male reproductive success by maximizing male paternity and preventing other males from inseminating a virgin female before the cohabiting male (Jackson 1986).

The occurrence of pre-mating cohabitation between adult males and subadult females may be constrained by several factors: (1) the overlapping of male and female maturation (Schneider 1997), (2) the male inability to assess the female developmental state, (3) the aggressiveness of subadult females towards males and (4) the lack of female sedentarism. Lycosids are commonly vagrant species, which would constrain pre-mating cohabitation in this family. However, a few lycosid species have adopted a life history in which immature individuals and adult females use burrows. In such species, mature males wander in search of females during the time of reproduction. Probably due to these sedentary habits, pre-mating cohabitation of adult males and subadult females has only been reported in burrowing lycosid species (*Geolycosa tu-*

Figure 1.—An adult male *Lycosa tarantula* at the entrance of the burrow of a subadult conspecific female, which can be observed beneath. In preparation for the photograph, the male was extracted from the female burrow, but the resulting posture is similar for the male when undisturbed. Initially, the male showed a highly aggressive response, while the female remained inside the burrow.

rricola (Treat 1880) Miller & Miller 1986, 1987). The description of cohabitation in *G. turricola* consisted of the finding of several males positioned face down at the entrance of female burrows during evening visits. In the lab, the extracted females turned out to be subadults. However, the authors were not able to report for how long adult males remain with subadult females in the field, nor could they describe the mechanisms used by males in finding females. In this note, we report the occurrence of pre-mating cohabitation between adult males and subadult females in another burrowing wolf spider (*Lycosa tarantula* (Linnaeus 1758)), consisting of a male who was observed to reside in the burrow of a subadult female continuously for six days. Contrary to vagrant males found to occupy burrows constructed by others, this male was not in the burrow for only a single day, and the burrow was not empty. We hypothesize that male *L. tarantula* may use tactochemical cues in finding subadult females.

In 1998, we conducted field observations as part of an ongoing study concerning the life history of this species in a 400 m^2 study plot located in Madrid (40°34′ N, 3°42′ W, central Spain). We visited the study plot twice daily for 56 d, comprising the whole mating season of the spiders. In this area, the species shows a relatively long post-embryonic development of 22 months, about 16 molts. Subadults of both sexes are sedentary, and males become vagrant after the maturation molt. We were able to follow the reproductive behavior of 18 subadults (9 males and 9 females). Thirty-six adult males were also followed. Spiders were captured by hand and individually marked with enamel by using a unique combination of yellow marks on their legs (Moya-Laraño 1999). Prior to marking, spiders were immobilized using a fine mesh and a drop of enamel was placed on the dorsal surface of 1 or 2 leg segments. Each leg segment corresponded to a numeric code, ranging from 1 to 9 (right legs) and 10 to 90 (left legs). The day of maturation was determined by the presence of the exuvia nearby the burrow entrance. Eight subadult females survived until maturation, and six of them survived until reproduction.

We recorded cohabitation of one adult male with one subadult female (11%, $n = 9$) in the female's burrow. The period of cohabitation was 6 complete days (a complete day was recorded when the spider was seen in the burrow at both the morning and the evening visits), and started 4 days before female maturation. The male generally exhibited a position at the upper part of the burrow and facing out (see Figure 1). It was extremely aggressive in response to our presence or manipulation. The two spiders

mated two days after female maturation. Soon after mating took place, the male left the burrow and started searching for a new female almost immediately. The male was observed to mate with a second female the following day.

Mating between the cohabiting pair was remarkable because the age at which the cohabiting female mated (2 d post-maturation molt, this study) was younger than that recorded both for non-cohabiting females in the same area (4–9 d post-maturation molt, pers. obs.) and for females kept under laboratory conditions (3–13 d post-maturation molt, pers. obs.). Furthermore, the cohabiting female did not mate with a second male. Our data revealed that 40% of non-cohabiting marked females in the field mated with two different males in the season. This indicates that the benefits of cohabitation for males could be related to ensuring the fertilization of a virgin female and perhaps also to reducing the likelihood that a female will mate a second time. The fertilization of a virgin female would secure the male's paternity only if there is strict first male sperm priority (Austad 1984), something that has not been completely demonstrated. Reduction of the likelihood of a female second mating might secure male paternity if there is sperm mixing.

The possible counterbalance costs for males may be twofold: (1) loss of mating opportunities, resulting from time spent during cohabitation, and (2) risks of being eaten by the host female. Sexual cannibalism by subadult females has been recorded during mating experiments in the lab (pers. obs.). However, in the case reported here, these costs were absent, since the cohabiting male was the only male observed to mate twice in the area ($n = 7$) and the female did not cannibalize the male.

Given the high benefits and the low costs, it is unclear why pre-courtship cohabitation rate was so low in our population. We suggest that molting synchrony between sexes is likely to be the underlying ecological factor influencing the occurrence of this phenomenon. Overall, males did not mature significantly earlier than females. As males spent a few additional days in their burrows before starting to search for females, their opportunities of finding subadult females might have been highly reduced.

In laboratory experiments, the interception of subadult female burrow silk elicits a strong courtship response by males. Available information suggests that males are unable to discriminate the developmental state of the females using chemical compounds bound to the female silk (Fernández-Montraveta & Ruano-Bellido 2000). Consequently, we hypothesize that the interception of burrow silk by males is a mechanism by which males may detect subadult female burrows in the field.

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SHORT COMMUNICATION

NEMATODE AND DIPTERAN ENDOPARASITES OF THE WOLF SPIDER *PARDOSA MILVINA* (ARANEAE, LYCOSIDAE)

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ABSTRACT. We collected 75 immature *Pardosa milvina* and maintained them in a laboratory until death or maturity to determine whether *P. milvina* in our population were harboring endoparasites. Nine mermithid nematodes emerged from *P. milvina* hosts, with each nematode emerging from a separate spider. One dipteran parasite, an acrocerid, emerged from *P. milvina*. This study provides the first published record of nematodes emerging from *P. milvina* and documents an additional record of acrocerid parasitism of *P. milvina*.

Keywords: Spiders, endoparasites, nematodes, acrocerids

The first report of nematode parasitism in spiders was in 1761 by Roesel (Poinar 1987). All reports of naturally occurring nematode/spider associations are for nematodes in the family Mermithidae (Poinar 1987). Rhabditoid nematodes, which naturally parasitize soil insects, have also been documented in spiders, but only in laboratory situations. However, since rhabditoid nematodes cause mortality within two to three days of entry, they may often be missed in the field (Poinar 1987). Mermithids cause behavioral and morphological changes in spiders, including slower reaction times to predators (Leech 1966), movement toward water (Poinar 1985, 1987), abdominal swelling, deformed epigyna, malformed legs and pedipalps, poor development of secondary sexual characteristics, and castration (Leech 1966; Poinar & Benton 1986).

Dipteran endoparasites of spiders are found in the families Tachinidae (Vincent 1985) and Acroceridae (Schlinger 1993). Acrocerids, small headed flies, are the only truly co-evolved and host-restricted endoparasitoids of spiders (Schlinger 1993). There are approximately 500 species in 50 genera of acrocerids, and the majority of larvae are endoparasites of spiders.

Pardosa milvina (Hentz 1844) is a lycosid spider with the largest females measuring approximately 6.2 mm in length, and the largest males measuring approximately 4.7 mm (Kaston 1981). These lycosids are found in dry, open woods and along the shores of ponds and streams from New England south to Georgia and west to the Rockies (Kaston 1981). To date, there are no records of endoparasitic nematodes from *P. milvina*, and the only acrocerid recorded from *P. milvina* is *Ogcodes eugonatus* (Eason et al. 1967; Schlinger 1993). Our study documents the first published record of nematodes emerging from *P. milvina*. We also report on an acrocerid emerging from *P. milvina*.

In 1998, we collected *P. milvina* at the Rock Springs Center for Environmental Discovery, Decatur, Illinois. We were collecting spiders for a behavioral study, and parasite emergence was an unexpected occurrence. We collected 75 immature spiders from the south shore of a pond from 1 June–9 July. None of the spiders had any noticeable external morphological abnormalities. Spiders were held individually in plastic petri dishes (14.5 cm diameter x 1.7 cm height) in a laboratory in Decatur, IL. We fed all spiders three times per week. Immature spiders received 12 fruit flies, *D. melanogaster*, at each feeding. As spiders reached the penultimate and adult stages, they received 2 houseflies, *M. domestica*, at each feeding. All spiders had constant access to water via saturated cotton balls.

We maintained all spiders in the laboratory until they either died or successfully molted to adulthood. As spiders died, we checked their arenas for the presence of nematode or dipteran parasites. Only two non-parasitized spiders died. Upon emergence, we immediately collected nematode parasites because juvenile mortality is high under laboratory conditions due to bacterial or fungal infections (Poinar 1987). Nematode parasites could only be identified to family because adult males are needed for identification to genus. Nematodes were identified by Dr. Robert P. Esser (Florida Dept. of Agriculture & Consumer Services, Gainesville,

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FL). Although we maintained an acrocerid parasite until maturity, it could not be identified to genus because of wing damage. The dipteran was identified by Dr. Peter H. Adler (Clemson University, Clemson, SC). Voucher specimens of host spiders, mermithids, and the single acrocerid have been deposited in The Field Museum of Natural History, Chicago, IL.

Nine mermithid nematodes emerged from *P. milvina* hosts, with each nematode emerging from a separate spider. All nematodes emerged from the spiders' ventral abdomen and were subsequently located in the spiders' saturated cotton balls. Nematodes emerged from 1–8 days after spider collection. Prior to emergence, there were no noticeable changes in host behavior or morphology. On 8 August, a dipteran parasite, an acrocerid, emerged from the abdomen of a penultimate female *P. milvina* that was collected on 16 June. Two days prior to acrocerid emergence, we noticed a change in the appearance of the hosts' book lung, and it is likely we were viewing the spiracles of the acrocerid. All ten spider hosts died within 24 hours of parasite emergence. All parasites emerged from immature spiders, although three spiders were penultimate females and one was a penultimate male.

Mermithid parasitism of lycosid hosts is an understudied area. Early researchers believed spiders were parasitized by mermithids when there were no suitable insect hosts available (Poinar 1987). It is currently believed that nematodes parasitizing spiders represent different species than those parasitizing insects (Poinar 1987); however, literature on nematode parasitism of spiders is scarce. Mermithids kill their spider hosts upon emergence, and their life cycle is largely unknown. Difficulty of nematode identification hinders progress. Adult males are required for species level identification, but adults are rarely collected because nematodes emerge from hosts as juveniles and are difficult to rear. After exiting the host, juvenile mermithids mature in soil or mud. Adults are non-feeding and live for a few days to months, depending on their stored food supply (Barnes 1980).

Although mermithids parasitize a diversity of spider families and approximately 20 lycosid species (Poinar 1987), this is the first record of a mermithid endoparasite in *P. milvina*. Minimal work has been conducted on the incidence of mermithid parasitism in a particular spider population. *Pardosa milvina* in our semi-aquatic pond habitat experienced 8% infection. Populations of *Pardosa glacialis* (Thorell 1872) in Canada experienced from 0–5% infection, with a greater incidence of infection in poulations near streams (Poinar 1987). A California population of *Atypoides riversi* O. P.-Cambridge 1883 exhibited 8% infection (Poinar 1987).

There are many spider taxa parasitized by acrocerids (Eason et al. 1967; Cady et al. 1993; Schlinger 1993), and strict host specificity is rare (Cady et al. 1993; Schlinger 1993). Acrocerids seek out cursorial or fossorial spider hosts or web builders that construct webs either close to the ground or with silk connections to vegetation (Cady et al. 1993). Female acrocerids oviposit in the environment and, upon hatching, larvae locate spider hosts, crawl to the abdomen or leg joints, and cut a small hole in the exoskeleton to enter the host. Larvae then migrate into the booklungs where they are exposed to oxygen (Schlinger 1993). Fourth instar larvae are the destructive stage because they actively feed on spider tissues from the legs, cephalothorax, and abdomen. *Lasiodora klugi* (C. L. Koch 1841), *Coras montanus* (Emerton 1890), and *Pardosa lapidicina* Emerton 1885 constructed atypical thick silk mats prior to acrocerid emergence, and acrocerid larvae subsequently used the mats for pupation (Cady 1984 in Cady et al. 1993; Eason et al. 1967). Larvae typically emerge from the spider's epigastric furrow, locate host silk, and use ventral abdominal spines to attach to the silk where they undergo pupation. Hosts usually die twelve hours prior to parasitoid emergence (Schlinger 1993).

Much remains to be discovered about the associations between endoparasites and their spider hosts. Parasitic occurrences should be reported because additional records may increase our understanding of the distribution, life cycle, and natural history of endoparasites and their possible impact on spider populations. We hope our results will stimulate others to report their finding and add to our our basic understanding of spider/parasitoid biology.

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SHORT COMMUNICATION

A NEW SUBSPECIES OF *PHILODROMUS RUFUS* (ARANEAE, PHILODROMIDAE)

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ABSTRACT. A new subspecies of *Philodromus rufus*, *P. r. jenningsi* is described from the south central and southeastern United States. It is characterized by a light brown unicolorous carapace, except for dark semicircular marks at the central rear carapace edge.

Keywords: *Philodromus rufus jenningsi*, crab spider, philodromid

The *Philodromus rufus* species-complex consists of 23 related species in America north of Mexico. Two species, *Philodromus exilis* Banks 1892, and *P. rufus* Walckenaer 1826, are very similar morphologically. Further, *P. rufus* comprises three subspecies in this region, and others in the Palearctic (Dondale & Redner 1968). About a decade ago it became apparent that an undescribed *Philodromus* occurred in northeastern Kansas. While genitalically indistinguishable from *P. rufus*, its color pattern was strikingly different from that of any member of the *P. rufus* group, and is closer to that of some members of the *P. aureolus* group, such as *P. keyserlingi* Marx 1890. More specimens have become available since then from the south central and south-eastern parts of the United States. Because the genitalia are identical to those of the other subspecies of *P. rufus*, and the males vibrate the front legs during courtship, it is appropriate to describe this taxon as a subspecies, since the currently known distribution is allopatric to that of any of the other subspecies. I wish to acknowledge Hank Guarisco, Lawrence, Kansas and Jamel Sandidge, Department of Ecology and Evolutionary Biology, University of Kansas who collected specimens of this subspecies and shared information with me, and Daniel T. Jennings, Garland, Maine who sent specimens of *P. exilis* and *P. rufus vibrans* Dondale 1964, for comparative study.

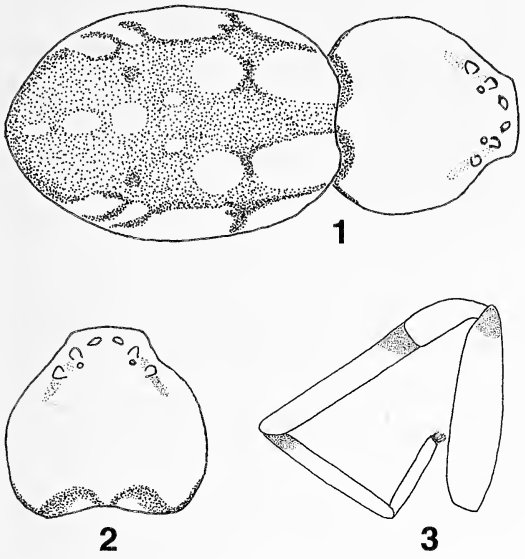
Philodromus rufus jenningsi new subspecies
Figs. 1–4

Material examined.—Holotype male: U.S.A.: KANSAS: *Douglas County,* Lawrence, University of Kansas, West Campus, 28 April 1995, B. Cutler, beating *Juniperus virginiana* L., deposited in Florida State Collection of Arthropods (FSCA), Gainesville, Florida.

Paratypes: All with same locality and habitat data as the holotype: 1♀, same data as holotype (deposited in FSCA); 1♂, 8 April 1995, matured 13 April 1995 (deposited in the American Museum of Natural History, New York(AMNH)); 1♀, 8 April 1995, matured 24 April 1995 (deposited in AMNH); 1♂, 28 April 1995 (deposited in the National Museum of Natural History, Washington, DC (NMNH)); 1♀, 2 April 1995, matured 17 April 1995 (deposited in NMNH); 1♂, 28 April 1995 (deposited in Museum of Comparative Zoology, Harvard University (MCZ)); 1♀, 8 April 1995, matured 18 April 1995 (deposited in MCZ); 1♂, 2 April 1995, matured 12 April 1995 (deposited in the Canadian National Collections, Ottawa (CNC)); 1♀, 2 April 1995, matured 16 April 1995 (deposited in CNC).

Other material examined: USA: ARKANSAS: Lonoke County, Prairie County; GEORGIA: Forsyth County (in winter webs of *Anelosimus studiosus* (Hentz 1850)); KANSAS: Douglas County (10 males and 17 females, same locality data as holotype, a few from woody vegetation other than *J. virginiana*), Jefferson County, Shawnee County; MISSISSIPPI: Lafayette County, Madison County, Marshall County (in winter webs of *A. studiosus*); NORTH CAROLINA: Gaston County (in winter webs of *A. studiosus*). Specimens in collections of the author, Hank Guarisco, and Daniel T. Jennings. Unless mentioned all were from *J. virginiana.*

Etymology.—This taxon is named for Dr. Daniel T. Jennings of Garland, Maine, USDA, Forest Service Insect Ecologist, retired. A well known spider ecologist and expert on crab spiders, and long time friend and colleague of the author, who first recognized these spiders as new.



Figures 1–3.—*Philodromus rufus jenningsi* new subspecies, female: 1. Dorsal view of prosoma and opisthosoma; 2. Dorsal view of prosoma; 3. Prolateral view of leg I.

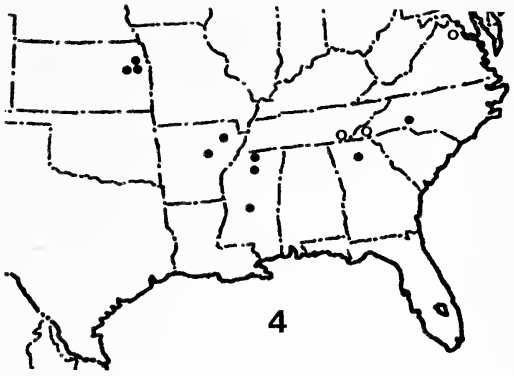


Figure 4.—Distribution of *Philodromus rufus jenningsi* in the south central and southeastern United States (filled circles); open circles are localities for *P. r. vibrans* from Dondale & Redner (1968).

Diagnosis.—The genitalic characters easily place this taxon in the *P. rufus* species complex. It may be distinguished from all other members of the complex by the solid light brown carapace with almost no markings except for the dark brown semicircular marks at the rear of the carapace, see Fig. 2. In the key to species and subspecies of the *P. rufus* group in Dondale and Redner (1968), this subspecies keys to couplet 3 where the color pattern does not match. Similarly in Dondale and Redner (1978) this subspecies keys to couplet 21 where again the color pattern does not match.

Description.—*Male*: Carapace 1.48 ± 0.11 (range 1.29–1.68) mm long and 1.47 ± 0.08 (range 1.25–1.58) mm wide; femur II 2.08 ± 0.25 (range 1.39–2.34) mm long (15 specimens). Carapace uniform light brown with two dark semicircular marks at rear center (Fig. 2). Legs I–III brown with dark speckling at distal end of femur, and at proximal ends of tibia and metatarsus (Fig. 3). Leg IV uniform light brown. Dorsum of opisthosoma in well marked individuals with a complex pattern (Fig. 1).

Female: Carapace 1.58 ± 0.13 (range 1.42–1.91) mm long and 1.52 ± 0.08 (range 1.32–1.62) mm wide; femur II 1.99 ± 0.17 (range 1.68–2.18) mm long (15 specimens). Coloration as in male but more clearly demarcated. Genitalia and leg spination as in other subspecies, see Dondale and Redner (1968). As in other subspecies of *P. rufus* males vibrate the first two pairs of legs during courtship and most habitat records are from woody vegetation.

Distribution.—The range of this subspecies (Fig. 4) is allopatric to all other known subspecies of *P. rufus* except in North Carolina. *P. rufus vibrans* occurs in the Smoky Mountains in the extreme southwestern part of that state, but at a higher elevation, not at the lower elevations where *P. rufus jenningsi* was taken.

Natural History.—Collector bias is marked in the records of *P. r. jenningsi*. Most records are from *J. virginiana*, because of the interest of the author and H. Guarisco in spiders from this conifer. The records from webs of the social theridiid spider *Anelosimus studiosus* resulted from the interest of Jamel Sandidge in that species. There are a few records from beating and sweeping broad-leaved shrubs and trees, and it is expected that, as in the other subspecies, *P. r. jenningsi* will be found to occur on woody vegetation throughout its range. In the laboratory, specimens of the later instars feed readily on species of *Drosophila* and other small insects and can easily be reared to maturity in small Petri dishes (55 mm in diameter by 15 mm tall). Courtship and mating observations were conducted in plastic tissue culture dishes 100 mm in diameter by 20 mm tall.

Courtship was initiated by males approaching females and rapidly vibrating the first and second pair of legs, see Dondale (1964) for details. Egg sacs made as a result of these laboratory matings were lenticular, about 10 mm in diameter, and attached to the surfaces of the Petri dishes. Up to three egg sacs may be made by mated females with the number of eggs decreasing in successive egg sacs. For the first egg sac, the mean number of eggs per sac was 16.6 ± 3.8, range 12–25 (15 egg sacs).

Attempts were made to assess fertility as a result of matings between specimens of *P. r. jenningsi* and specimens from two populations of *P. r. vibrans* (MAINE: Penobscot County and MINNESOTA: Ramsey County). There were some cross

population matings, but the numbers were low and resulted in few fertile eggsacs. Future attempts using larger cages such as those utilized by Dondale (1964) may be more productive.

Remarks.—Pattern intensity varies considerably in *P. r. jenningsi*. Well-marked specimens resemble those in Figs. 1–3. Other individuals have the pattern reduced. Extreme reduction results in a loss of all pattern, except for the dark semicircular marks at the rear of the carapace. Immature specimens of *P. r. jenningsi* closely resemble immature specimens of *P. keyserlingi*, and both are found on foliage of *J. virginiana*. Except for the earliest instars, specimens of the latter species have a thin black margin around the carapace which is lacking in the former species, except at the very rear of the carapace.

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SHORT COMMUNICATION

A NEW SPECIES OF THE SPIDER GENUS *ANYPHAENOIDES* FROM BRAZILIAN CAATINGA (ARANEAE, ANYPHAENIDAE, ANYPHAENINAE)

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ABSTRACT. *Anyphaenoides locksae*, a new species from Brazilian "caatinga", in Central, state of Bahia, is described.

Keywords: Araneae, Anyphaenidae, Anyphaeninae, *Anyphaenoides*, neotropical region

To date, 14 species of the genus *Anyphaenoides* have been described from the Neotropical region (Brescovit 1992, 1997, 1998; Baert 1995). During an expedition to the central region in the state of Bahia, Brazil, we collected specimens of a new species that might be endemic to the "caatinga" region (Ab'Saber 1977; Joly et al. 1999) in northeastern Brazil.

This is the second paper describing spiders collected in the Brazilian "caatinga" as a result of the Central project. This project was developed by the staff of the Archaeology Department of the Museu Nacional do Rio de Janeiro. Further details on the project and study area may be found in Brescovit & Ramos (in press).

The types and material examined are deposited in the collections of the Instituto Butantan, São Paulo (A.D. Brescovit, IBSP) and Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro (A.B. Kury, MNRJ). Description follows Brescovit (1998). All measurements are in millimeters. The female epigynum was submerged in clove oil in order to study the internal structures.

Anyphaenoides locksae new species
Figs. 1–4

Types.—Male holotype and female paratype from Riacho Largo (11°13′55″S, 42°11′28″W), Central, Bahia, 19 September 2000, A.D. Brescovit, deposited in IBSP 26139; paratypes: 2 ♂ and 2 ♀ with same data as holotype, E.F. Ramos col., deposited in IBSP 26141 and MNRJ.

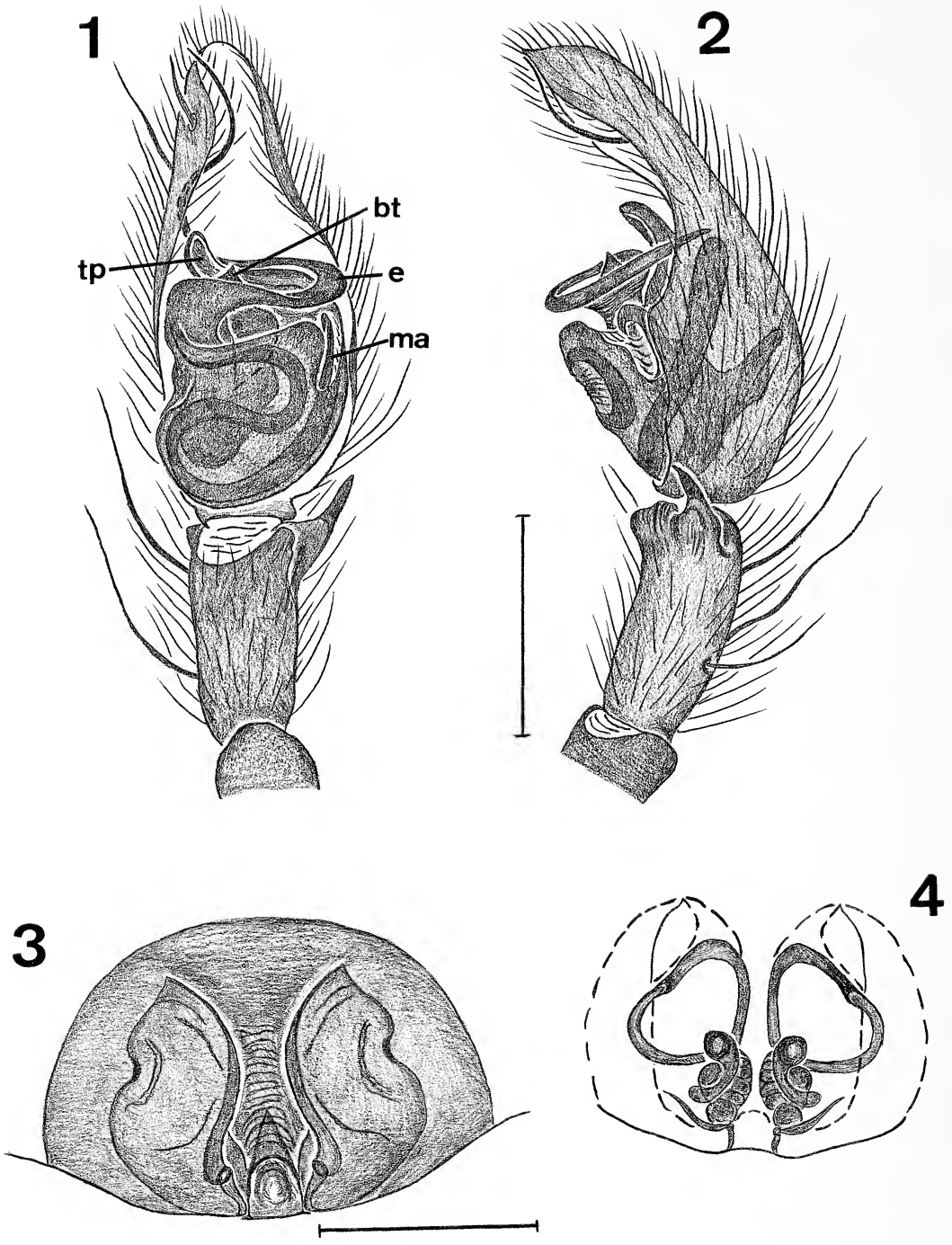
Etymology.—The specific name is a patronym in honour of Dr. Marta Locks, archaeologist of the Museu Nacional do Rio de Janeiro, who helped the authors during the Central collecting expeditions.

Diagnosis.—*Anyphaenoides locksae* may be distinguished from other species of this genus by the spoon-like tegular projection (Fig. 1) and the narrow, truncated projection at the base of the retrolateral tibial apophysis (Fig. 2) on the male palp; and the sinuous atrium and larger basal hood in the female epigynum (Fig. 3).

Description.—Male (holotype): Carapace orange, with grayish green paramedian bands and black eye borders. Chelicerae reddish brown. Labium and endites orange. Sternum yellowish with grayish border. Legs yellow with ventral distal area of femora I and II grayish. Abdomen cream colored, with lateral border grayish, dorsally with six to eight pairs of grayish green spots on posterior third.

Total length 3.40, carapace length 1.40, width 1.10, clypeus height 0.06. Eye diameters and interdistances: AME 0.08, ALE 0.10, PME 0.12, PLE 0.10; AME–AME 0.04, AME–ALE 0.04, PME–PME 0.10, PME–PLE 0.08, AME–PLE 0.04. MOQ length 0.28, front width 0.16, back width 0.28. Chelicerae 0.76 long, with 4 promarginal teeth and 6 retromarginal denticles. Epigastric furrow 0.45 from tracheal spiracle, spiracle 0.70 from base of spinnerets.

Leg measurements: Leg I; femur 1.32, patella 0.52, tibia 1.32, metatarsus 1.12, tarsus 0.52, total 4.80. Leg II; 1.12, 0.48, 0.96, 0.88, 0.44, 2.28. Leg III; 0.88, 0.40, 0.68, 0.84, 0.32, 3.12. Leg IV; 1.44, 0.44, 1.08, 1.24, 0.36, 4.56. Leg spination: tibia I v2–2–0, p0, r0; II v0–1r–0, p0–1–0, r0; III v0–1p–1r, p1–1–0; IV v0–2–2, p1–1–0; metatarsus II r0;



Figures 1–4.—*Anyphaenoides locksae* new species, male palp: 1. ventral view; 2. retrolateral view; female epigynum, 3. ventral view; 4. dorsal view. Abbreviations: bt, basal teeth of embolus; e, embolus; ma, median apophysis; tp, tegular projection. Scale bars = 0.25 mm.

III v2–0–2. Palpal tibial retrolateral apophysis narrow with acute tip (Figs. 1, 2); embolus very wide at base, distally narrowed, sinuous, with short, triangular basal tooth; tegulum with conspicuous apex (Fig. 1).

Female (allotype): Coloration as in male, except abdomen darker. Total length 3.75, carapace length 1.60, width 1.15, clypeus height 0.06. Eye diameters and interdistances: AME 0.08, ALE 0.12, PME 0.06, PLE 0.12; AME–AME 0.06, AME–ALE 0.04, PME–PME 0.10, PME–PLE 0.08, ALE–PLE 0.04. MOQ length 0.28, front width 0.32, back width 0.44. Chelicerae 0.66 long, with four promarginal teeth and seven retromarginal denticles. Epigastric furrow 0.76 from tracheal spiracle, spiracle 1.40 from base of spinnerets.

Leg measurements: Leg I; femur 1.28, patella 0.56, tibiae 1.08, metatarsus 0.92, tarsus 0.52, total 4.36. Leg II; 1.08, 0.48, 0.92, 0.80, 0.40, 3.68. Leg III; 0.88, 0.36, 0.60, 0.80, 0.28, 2.92. Leg IV; 1.40, 0.56, 1.04, 1.36, 0.40, 4.76. Leg spination: tibia I v1p–2–0, p0, r0; II v0, p0, r0; III v0–1p–0, p0–1–0, r0–1–0; IV v0–1p–2, p1–1–0; metatarsus II p0, r0; III v1r–0–2; IV v1p–0–2. Epigynum with lateral border very large, presenting median sinuosity (Fig. 3). Spermathecae oval, very close to each other, with irregular border; copulatory ducts long, coiled apically and laterally; fertilization ducts elongated, very thin (Fig. 4).

Variation.—Six ♂: total length 3.35–4.10; carapace 1.40–1.75; femur I 1.28–1.60; chelicerae 0.62–1.05; retromarginal denticles of chelicerae 5–7. Seven ♀: total length 2.80–4.40; carapace 1.30–1.60; femur I 0.92–1.28; retromarginal denticles of chelicerae 6–7.

Natural history.—All material was collected with beating trays. The specimens from Central city were collected on the medium stratum of the riparian forest (called "mata ciliar" in Brazil). The other specimens were collected on the foliage in the dry margin of the Riacho Largo near Central, Bahia during the day.

Distribution.—Known only from the type locality in Bahia, Brazil.

Additional material.—BRAZIL. *Bahia*: Central (11°13′55″S, 42°11′28″W), 1 female, 20 September 2000, A.D. Brescovit (IBSP 26142); (Riacho Largo), 2 ♂, 1 ♀, 19 September 2000, A.D. Brescovit & E.F. Ramos (IBSP 26144; 26143; 26140).

ACKNOWLEDGMENTS

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2003. The Journal of Arachnology 31:148–150

SHORT COMMUNICATION

A NEW SPECIES OF *AUSTROCHILUS* FROM CHILE (ARANEAE, AUSTROCHILIDAE, AUSTROCHILINAE)

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ABSTRACT. *Austrochilus forsteri* new species, (Araneae, Austrochilidae, Austrochilinae) is described and illustrated based on specimens collected in Malleco Province, Chile.

RESUMEN. *Austrochilus forsteri*, nueva especie, (Araneae, Austrochilidae, Austrochilinae) es descripta e ilustrada sobre la base de especímenes colectados en la provincia de Malleco, Chile.

Keywords: Austrochilidae, *Austrochilus*, taxonomy, Chile

The Austrochilinae include two genera endemic to the Andean forests of central and southern Chile and adjacent Argentina. They comprise (along with the Hickmaniinae and Gradungulidae) the superfamily Austrochiloidea, sister group of Araneoclada (all araneomorph spiders other than Hypochilidae) (Forster et al. 1987).

During recent field work in Chile, two of us (LL and CG) observed austrochiline biology, mainly the combing and web-building behavior (Lopardo et al., unpub. data). When the material was determined, we found that the specimens from Monumento Natural Contulmo did not belong to any of the previously described species (Forster et al. 1987). In the present note we describe this new species, which seems to be close to *Austrochilus manni* Gertsch & Zapfe 1955, *A. melon* Platnick 1987, and *A. schlingeri* Platnick 1987 (see below). Behavioral and ecological data will be detailed elsewhere (Lopardo et al., unpub. data).

Specimens are deposited in the Museo Nacional de Historia Natural, Santiago, Chile (MHNS, Ariel Camousseight), Museo Argentino de Ciencias Naturales, Buenos Aires (MACN, Cristina L. Scioscia) and the American Museum of Natural History, New York (AMNH, Norman Platnick). The format of the descriptions and abbreviations follows Forster et al. (1987). The female genitalia were partially digested with KOH solution to dissolve the soft tissues and then observed with a compound microscope. Measurements are expressed in millimeters.

Austrochilus forsteri new species
(Figs. 1–8)

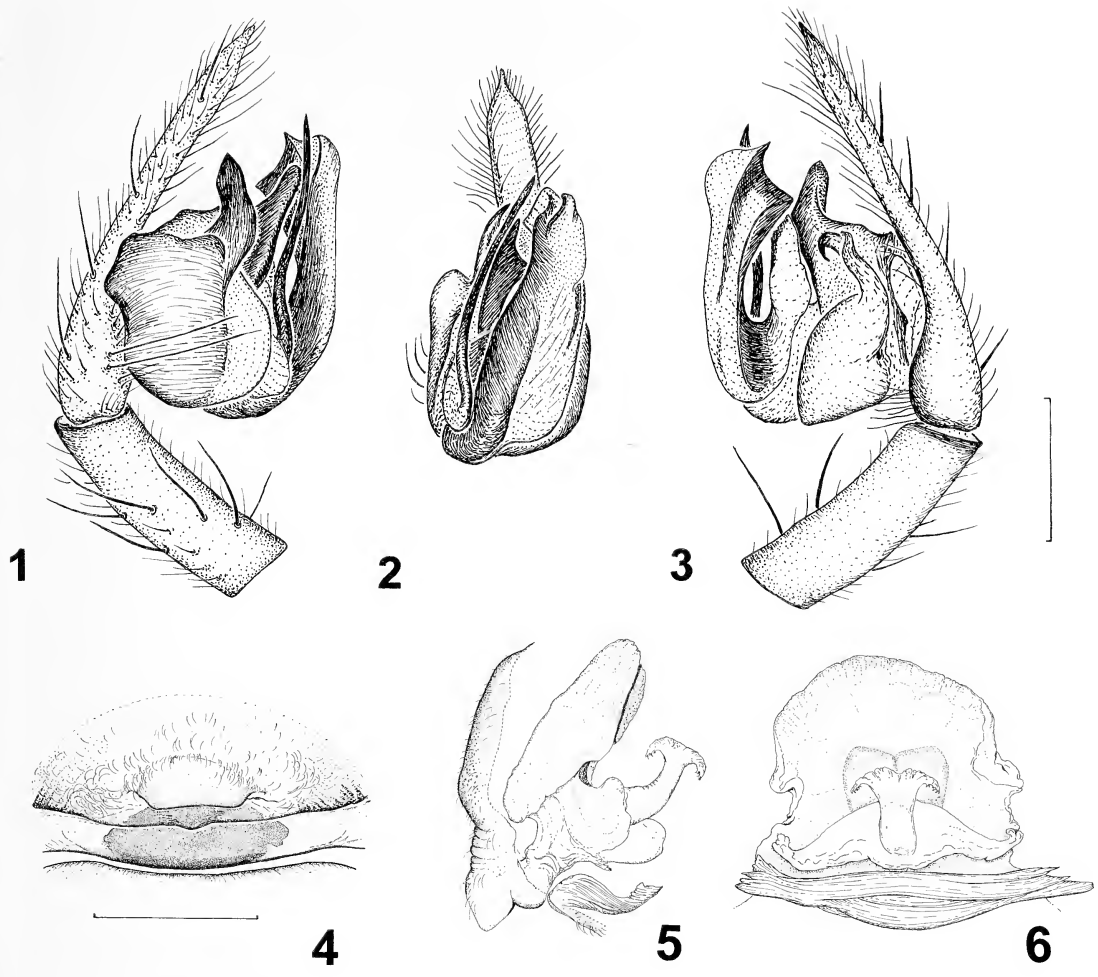
Thaida peculiaris (misidentification): Forster et al. 1987: 44 (records for Monumento Natural Contulmo only).

Types.—Male holotype and female paratype from Monumento Natural Contulmo, elev. 340 m, Malleco Province, Región IX (Araucanía), Chile (38°01′S, 73°11′W) 19–21 December 1998, M.J. Ramírez, L. Lopardo, L. Compagnucci, C.J. Grismado (MHNS).

Note.—The types were found together in the female's web, with some kleptoparasitic anapids (*Sofanapis antillanca* Platnick & Forster 1989). This interspecific relationship was reported recently (Ramírez & Platnick 1999).

Etymology.—The specific name is a patronym in honor of the late Dr. Raymond Forster, in recognition of his fundamental contributions to our knowledge of the spiders of the southern Hemisphere.

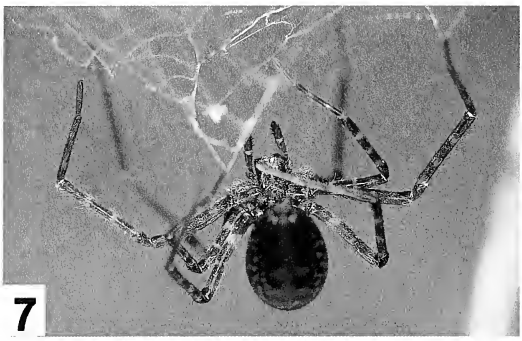
Diagnosis.—Males resemble those of *A. manni*, *A. melon* and *A. schlingeri* in having a sclerotized strip retrolaterally on the male palpal conductor (Fig. 3, Forster et al. 1987, figs. 126, 132, 138), but differ by the thin and sinuous embolus and by the shape of the tip of the conductor. Females resemble those of *A. franckei* Platnick 1987 in having the epigynum with a broad oval sclerotized plate (Fig.



Figures 1–6.—*Austrochilus forsteri* new species: 1–3, left male palp; 1, prolateral; 2, ventral; 3, retrolateral; 4–6, female epigynum; 4, ventral view; 5, cleared, lateral view; 6, cleared, dorsal view. Scale bars = 1 mm.

4) but differ in the shape of internal genitalic structures (Figs. 5, 6).

Description.—Male (holotype): Total length 10.76; carapace: 5.66 long, 3.88 wide; light brown, dusky ocular area, longitudinal midline dusky brown, sides lighter, with two yellowish paraxial bands. Design of dark lines from PME shaped like a posteriorly directed arrow. Clypeus at middle about 3.5 times AME diameter in height; eye diameters and interdistances: AME 0.20; ALE 0.32; PME 0.32; PLE 0.34; AME–AME 0.12; AME–ALE 0.12; PME–PME 0.10; PME–PLE 0.08; ALE–PLE 0.04; AME–PME 0.20; MOQ: 0.76 length, 0.60 front width, 0.84 back width; endites reddish brown except white anteromedian surfaces, labium dark brown except for white anterior margin, sternum uniform brown. Legs without distinct band pattern, all yellowish brown except tibiae, metatarsi and tarsi I–II, reddish brown. Leg formula: 1243; measurements: length 1–4: femora: 9.94, 7.82, 6.19, 7.33; patellae: 1.95, 1.79, 1.46, 1.63; tibiae: 10.75, 6.84, 4.72, 6.19; metatarsi: 10.27, 7.49, 5.05, 6.52; tarsi: 3.42, 2.60, 2.12, 3.09; palp: femur length 2.58, patella length 0.89, tibia length 1.53, cymbium length 2.91. Spination (only surfaces bearing spines listed): femora: I d1–0–0, p2–3–2, r2–2–2; II d1–1–0, p1–2–3, r2–2–2; III, IVd1–1–1, p1–2–2, r2–2–2; patellae: III p0–1–0, r0–1–0; IV p0–1–0; tibiae: I d0–0–1, p2–3–2, v4–4–4, r2–2–2; II d0–1–0, p1–2–2, v4–4–2, r1–2–1; III d1–1–1, p1–1–1, v2–2–2, r0–1–2; IV d0–1–1, p2–2–3, v2–2–2, r2–2–2; metatarsi: I p1–2–0, v3–2–2, r1–1–0; II p1–2–1, v2–3–2, r1–1–2; III p1–2–1, v3–2–2, r2–1–2; IV p2–0–1, v1r–2–2, r1–0–2; palp: femur d0–0–1, p0–0–1, r0–0–1; patella d0–0–1; tibia d1–1–0, p1–1–0, v2–0–0. Abdomen purplish brown at dorsum and sides; venter with light spots in paramedian, longitudinal rows between book-



Figures 7–8.—*Austrochilus forsteri* new species, living specimens: 7, female; 8, female feeding on an insect with some kleptoparasites (*Sofanapis antillanca*). (Photographs: Martín J. Ramírez.)

lungs and tracheal patches. Palp (Figs. 1–3): large prolateral tegular apophysis; embolus thin and gently sinuous, apically ridged; terminal apophysis distally serrated; massive conductor with a retrolateral sclerotized tip.

Female (paratype): As in male, except as noted: total length 13.86; carapace: 6.30 long, 4.93 wide; clypeal height about 2.6 times AME diameter; eye diameters and interdistances: AME 0.30; ALE 0.40; PME 0.32; PLE 0.36; AME–AME 0.10; AME-ALE 0.14; PME–PME 0.34; PME–PLE 0.20; ALE–PLE 0.02; AME–PME 0.22; MOQ: 0.90 length, 0.62 front width, 0.78 back width; two dark, thin streaks extending back from PME to about half of pars cephalica. Legs yellowish brown with lighter bands on femora, patellae and tibiae (except tibiae I, uniformly reddish brown), metatarsi and tarsi uniformly reddish brown, III and IV slightly lighter. Leg formula: 1243; measurements: length 1–4: femora: 9.45, 7.66, 5.70, 7.17; patellae: 2.44, 2.44, 1.63, 1.95; tibiae: 9.78, 7.49, 4.56, 6.52; metatarsi: 8.31, 6.84, 5.21, 6.03 (calamistrum length 2.16); tarsi: 3.09, 2.28, 1.95, 2.60; Palp: femur length 3.07, patella length 1.05, tibia length 1.69, tarsus length 3.15. Spination: femora: I d1–0–1, p1–3–2, r2–3–1; II d1–1–1, p1–2–2, r2–3–1; III d1–1–1, p1–2–2, r2–1–2; IV d1–1–1, p1–2–1, r2–2–2; tibiae: I d0–1–0, p2–3–2, v4–4–2, r1–2–1; II d0–1–0, p1–1–2, v2–4–2, r1–2–1; III d1–1–1, p1–1–1, v3–2–2, r0–1–1; IV d1–1–1, p1–1–1, v2–2–2, r1–1–2; metatarsi:I p1–1–1, v2–4–2, r1–2–2; II p1–2–1, v4–2–2, r1–1–2; III p1–2–1, v3–2–2, r2–1–2; IV p2–1–1, v2–2–2, r2–1–2. Palp: femur d0–1–2, p0–0–1, r0–0–2; patella d0–0–1; tibia d1–1–0, p1–1–0; tarsus d1–1–0, p1–1–0, v4–0–2, r2–1–0. Female genitalia (Figs. 4–6): Wide and oval sclerotization behind the anterior knob; internally, anterior lobe with conspicuous pore plate; distal extension of median lobe with ragged borders; posterior receptaculum flattened and transversally folded.

Material examined.—Same data as the types: 1 ♂ (MACN 9837); 1 ♀ (MACN 9838); 1 ♀ (MACN 9839) (MJR 19.XII.98/11, photo frames 27/30); 1♀, 4 juveniles (MACN 9845); 1♀, 2 juveniles (MHNS); 1 juvenile (MACN 9846); 1 juvenile (MACN 9844) (MJR 19.XII.98/7, photo frames 13/20); 1 juvenile (MACN 9842); 1 juvenile (MACN 9847) (MJR 19.XII.98/9, photo frame 26); 1 juvenile (MACN 9841); 1 subadult ♂ (MACN 9840); 1 juvenile (MACN 9843); 1 subadult ♀ (MHNS); 2 juveniles (MHNS); same locality, elev. 425 m, montane forest, 23 January 1985, N.I. Platnick & O.F. Francke, 1 ♀, 3 subadult ♂, 3 juveniles (AMNH).

Distribution.—Known only from the type locality.

ACKNOWLEDGMENTS

We wish to thank CONAF for authorization to work in Chilean protected areas; Don Ismael Matamala, the park keeper at Monumento Natural Contulmo, was especially helpful in the field; Mohammad U. Shadab inked the palp drawings; Mark S. Harvey, Martín J. Ramírez and two anonymous reviewers provided critical comments on a draft of the manuscript; MJR also took the photographs of living specimens that illustrate this paper. The field trip to Chile was supported by Sigma-Xi through a Grant-in-Aid to Lara Lopardo.

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2003. The Journal of Arachnology 31:151–153

SHORT COMMUNICATION

METAZYGIA LEVII, A NEW SPECIES OF ORB-WEAVING SPIDER FROM BRAZIL (ARANEAE, ARANEIDAE)

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ABSTRACT. A new species of orb-weaving spider, *Metazygia levii*, is described and illustrated based on specimens from State of Espírito Santo, Brazil.

Keywords: *Metazygia*, Araneidae, neotropical region, taxonomy

The family Araneidae, when compared with other large spider families, is certainly the best known in the neotropics. This privileged situation can be attributed to Herbert W. Levi's excellent revisions (see complete series citations in Levi 1993, 1996, 1999, 2001). These revisions not only allow species identification, but also enables us to recognize new species, which is impossible in unrevised groups. Even in such a well known group, new species are eventually discovered. In this paper, a new species of *Metazygia* F.O.P.-Cambridge 1904, collected during a spider diversity inventory, is described and illustrated. The material examined was deposited in the spider collection of Instituto Butantan (curator, A. D. Brescovit). All measurements are in mm.

Metazygia levii new species
Figs. 1–5

Types.—Male holotype from Reserva Florestal da Companhia Vale do Rio Doce, São Mateus, Espírito Santo, Brazil (19°06′S, 39°45′W), 19–25 July 1997, A. D. Brescovit et al. (IBSP 29315); male and female paratypes, same collection data (IBSP 12768).

Etymology.—The specific name is a patronym in honor of H.W. Levi, in recognition of his contributions to neotropical spider systematics.

Diagnosis.—Males of *Metazygia levii* resemble those of *M. gregalis* (O.P.-Cambridge 1889), *M. benella* Levi 1995 and *M. yobena* Levi 1995 in the medium-sized embolus and the conductor with ventral prongs (Levi 1995, figs. 258, 267 & 274), but differs by the presence of an ectal pointed projection in the tegulum and the sub-pentagonal median apophysis (Fig. 2–M). Females can be distinguished from all other species of the genus by the epigynum with large and sclerotized lateral plates (Figs. 3, 4–L) and with a ventrally projected median field (Fig. 5–MF) with a small scapus (Fig. 5–S).

Description.—Male (paratype): Carapace orange, cephalic region brown, chelicerae brown. Labium and endites light brown. Sternum orange with pale brown spots. Coxae and femora light orange; trochanters, patellae, tibiae, metatarsi and tarsi reddish-brown. Dorsum of abdomen gray with dark sinuous lateral stripes, laterally dark, venter uniformly dark. Total length 4.7, carapace length 2.3, width 1.7. Tibia I length 1.7, II 1.6, III 0.85, IV 1.0. Abdomen length 2.3, width 1.8. Cymbium semi-transparent in mesal view, radix small, conductor sclerotized, pointed ventrally and with a mesal soft branch supporting the embolus. Conductor soft branch with two ventral prongs. Median apophysis sub-retangular, with a central white area and a pointed and sclerotized apex (Fig. 2–MA). Tegulum with a sclerotized and ventrally pointed flange (Fig. 2–EP).

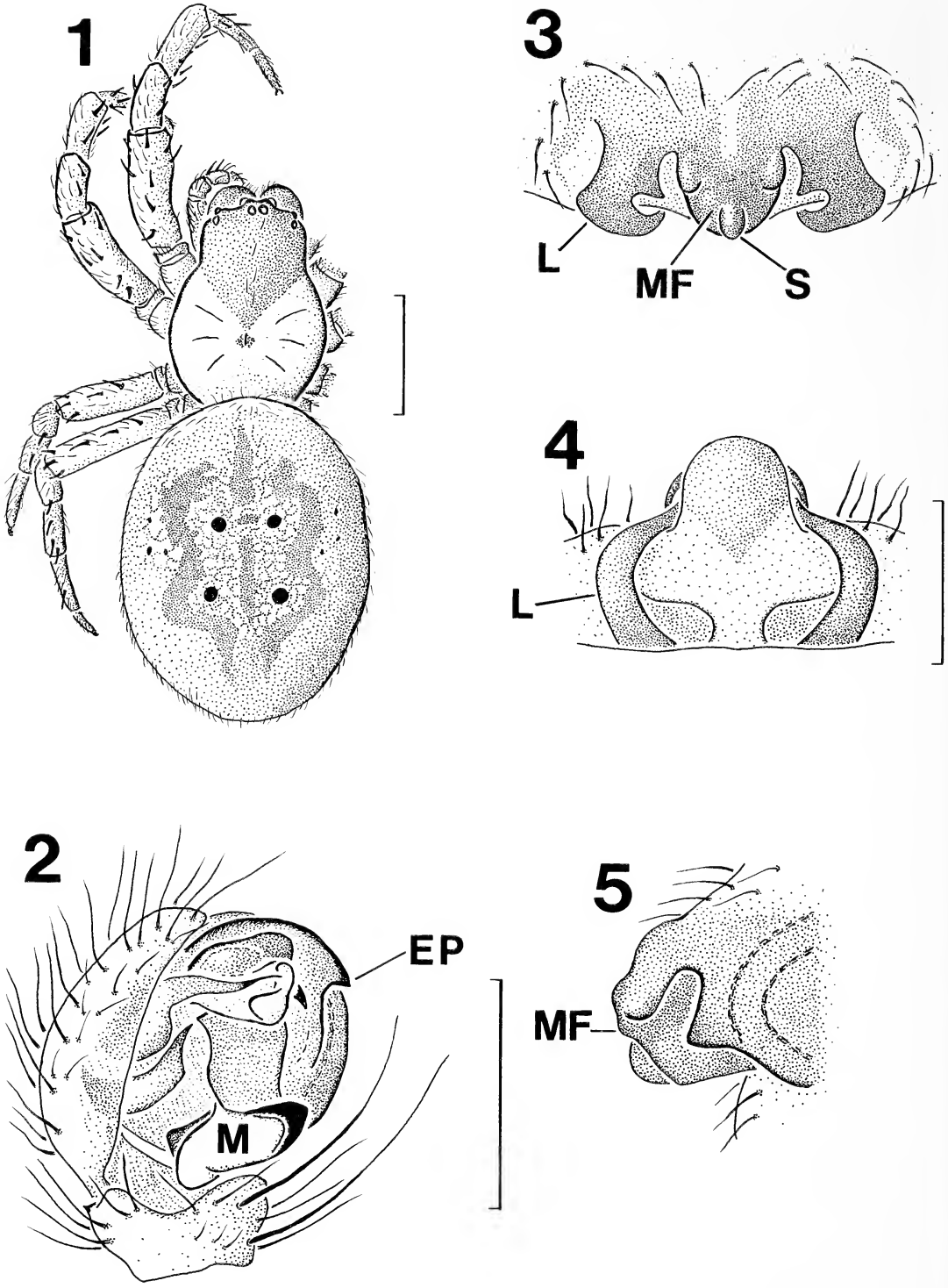
Female (paratype): Color as in male, but darker (Fig. 1). Total length 6.57, carapace length 2.57, width 2.14. Tibia I length 1.70, II 1.42, III 0.71, IV 1.14. Abdomen length 4.71, width 3.42. Epigynum with large lateral sclerotized plates, and ventrally projected median field (Fig. 3). Median plate cross-shaped, rounded apically (Fig. 4). Median field with a small ventral rounded projection (Fig. 5).

Variation.—Females, total length 6.0–8.57 (n = 6).

Natural History.—Two females were collected in a vegetation type composed mainly by scattered patches of small bushes over a sandy soil, locally know as "Campo Nativo" (Jesus 1988).

Distribution.—Known only from the type locality.

Additional material.—Three immature specimens collected with the types (IBSP 12768); 5 ♀, same locality as types, 19–25 July 1997 (IBSP 12951); 2 ♀, same locality as types, 5–12 January 1998 (IBSP 29316 & IBSP 16570).



Figures 1–5.—*Metazygia levii* new species. 1. Female body, dorsal view; 2. male palpus, mesal view; 3. female epigynum, ventral view; 4. posterior view; 5. lateral view. Scale lines: 1 = 2 mm; 2 = 0.5 mm; 3–5 = 0.25 mm. Abbreviations: EP, ectal pointed projection of tegulum; L, lateral plate; M, median apophysis; MF, median field; S, scapus.

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The author is indebted to Antonio D. Brescovit for providing specimens of *Metazygia gregalis* for comparison, to Cristina A. Rheims and A.D. Brescovit for suggestions on the first draft of the manuscript, and the staff of Reserva Florestal da Companhia Vale do Rio Doce for support in field work. This paper received financial support from Fundação de Amparo à Pesquisa do Estado de São Paulo PhD fellowship (FAPESP 99/05695-8).

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SHORT COMMUNICATION

FISHING BEHAVIOR IN A GIANT WHIP SPIDER

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ABSTRACT. Whip spiders (Amblypygi) are a small and understudied group of arachnids characterized by long antenniform legs and raptorial pedipalps. Due to their nocturnal habits, secretive nature and geographical distribution there have been very few studies of feeding behavior in this group. Here, we report a remarkable foraging strategy adopted by the giant tropical whip spider *Heterophrynus cheiracanthus* (Gervais 1844) inhabiting rocky outcrops adjacent to mountain streams running through primary tropical rainforest on the Caribbean island of Tobago. *Heterophrynus cheiracanthus* positions itself close to the stream edge on a vertical rock surface with pedipalps fully extended and antenniform legs frequently entering the shallow water. Freshwater prawns of the genus *Macrobrachium* are caught while still submerged in the water despite the whip scorpion being unable to use the trichobothria on the walking legs. Possible mechanisms of prey detection are discussed.

Keywords: Amblypygi, Tobago, predation

Whip spiders (Chelicerata, Amblypygi) are a numerically small and little studied taxon of arachnids consisting of about 120 species that are restricted to the tropics and sub-tropics (Weygoldt 2000). They are characterized by strong raptorial pedipalps and thin antenniform forelegs bearing numerous multiporous sensilla and chemoreceptors making them exceedingly sensitive to both vibrations and olfactory cues (Igelmund & Wendler 1991; Hebets & Chapman 2000b; Hebets 2002). Moving prey are generally detected by the trichobothria on the walking legs while the feelers are primarily used to chemically investigate prey and to assist in distance recognition (Weygoldt 2000). Whip spiders with antenniform legs but without trichobothria can find only dead or slowly moving prey items (Weygoldt 2000).

Certain generalizations can be made from the few field studies that have been conducted on whip spider ecology and behavior (reviewed in Weygoldt 2000). All species are flattened with long legs and can move extremely quickly in attack and defence. They are often found under the bark of trees (Hebets 2002) or within rock crevices during the day. At night they emerge from their refuges to hunt for arthropods and even small vertebrates such as frogs and lizards (Reagen & Wade 1996; Kok 1998). The fearsome looking raptorial pedipalps are armed with an array of large spines, which are used to impale and immobilize prey. In the Phrynichidae, the distal parts of the tibia and the tarsus form hand-like chelae. Once captured, the prey is transferred to the mouth for dissection and ingestion. Like many large arachnids amblypygids do not possess a toxic bite and rely on speed, agility and strength to overpower prey.

Very few studies of amblypygids feeding under natural conditions have been made (see Hebets 2002 for notable exception) leading Weygoldt (2000, p 52) to state that "for most species the food consumed under natural conditions is unknown". This is mainly due to the difficulty of studying such secretive, nocturnal animals and the apparent infrequency with which they feed.

One particularly large (maximum body length 35 mm) and aggressive amblypygid, *Heterophrynus cheiracanthus* (Gervais 1844), can be easily found on the large rocks at the margin of mountain rainforest streams on the island of Tobago, off the Northeast coast of Venezuela (Ladle pers.obs.). Some of the least known amblypygids occur in the tropical forests of the Caribbean (Browne 1992) and *H. cheiracanthus* is no exception, with virtually no published information about its ecology and behavior. Over five field trips between 1999 and 2002 we made 320 observations over 35 nights that support the suggestion that this species, uniquely among amblypygids, regularly "fishes" for prawns in the rainforest streams adjoining the rocky outcrops on which they reside.

The data for our study of the fishing behavior of this species comes from several sources. First, ob-

servations of relative position and hunting behavior provide indirect evidence of its preferred prey. Large *H. cheiracanthus* are highly nocturnal and emerge from deep rock crevices as soon as the sun goes down. Mountain streams in Tobago are prone to frequent spates during the wet season and often have very steep sides incorporating huge slabs of metamorphic rock. The amblypygids share these vegetationless rock faces with a few small grapsid crabs although they were never observed to hunt or eat these either in the field or the laboratory.

During nocturnal sampling of streams in Castara and Little Englishmans Bay on the north side of Tobago several observations were made relating to the orientation and positioning of *H. cheiracanthus* relative to the watercourse. A total of 320 (60 adult male, 82 adult female, 178 sub-adults) observations of whip spiders on bare rock surfaces were made in which both adult males (68.3%) and adult females (52.4%) appeared to prefer vertical stone surfaces. In the vast majority of observations of males (66.6%), females (73.2%) and sub-adults (92.1%) on vertical surfaces individuals were found to be orientated directly towards the stream. Juvenile amblypygids were never seen on rock faces during the night (possibly due to potential cannibalism) but could be found at low densities during the day under accumulations of leaf litter and detritus. Both sexes were normally observed close to the water (mean distance from stream (mm) ± standard deviation; males 178.64 ± 113.78, $n = 22$; females 104 ± 92.23, $n = 23$). On 12 occasions individuals were actually observed with their extended forelegs under the water and their raptorial pedipalps raised and parted in the characteristic active hunting position.

Although some amblypygids have been reported to enter water bodies breathing through a plastron (Hebets & Chapman 2000a) we never observed any individuals with more than their antenniform forelegs immersed. This is interesting since prey detection is normally through trichobothria on the walking legs and the feelers are generally only involved with chemoreception. One possible explanation is that prey are detected when they come into physical contact with the antenniform legs. Since the density of *Macrobrachium* may exceed 200 per m^2 (Ladle pers. obs.) in these rainforest pools such contact would not be unusual. An interesting corollary to this is that both prawn and whip spider abundance appears to be lower in section of stream occupied by mountain mullet (*Agonostomus monticola*), a voracious predator on freshwater prawns (Ladle pers.obs.).

The results of laboratory feeding experiments to test the suggested behaviors were inconclusive. While in Tobago, two captive individuals were observed to feed on grasshoppers although no such insects were ever observed on the rock faces. They ignored grapsid crabs completely. It has so far proved impossible to keep prawns alive for long enough in still water to conduct controlled experiments.

Finally, we gained evidence of fishing behavior from two rare direct observations. Although amblypygids, like many large, long lived insects eat very infrequently, we have observed two instances of individuals (one male and one female) consuming recently caught prawns. On one of these occasions the capture was witnessed: an amblypygid was seen with its antenniform legs dipping in the water and its pedipalps raised in the typical hunting posture. A rapid strike into 2–3 cm of water resulted in the capture of a medium sized *Machrobrachium* (carapace width 5–10 mm approx.). This is the first reported direct observation of prawn capture in the arachnida as far as we can determine. Voucher specimens from this study are deposited in the Stuttgarter Museum für Naturkunde, Germany.

Prawn eating behaviour has only been described in one other species of arachnid, *Trechalea extensa* (O. P.-Cambridge 1896) (Trachaleidae), that inhabits small streams in the northwest of Costa Rica (Van Berkum 1982). Large individuals were seen hunting for and devouring the abundant freshwater prawns within these streams although actual capture was never observed in the field or the laboratory. The prey capture mechanism in these spiders seems to be very similar to that of *H. cheiracanthus*. Van Berkum (1982) watched prawns swim very near the spiders with no apparent reaction on the part of the spider and was left concluding that prey capture only occurred when the legs of the spider had been brushed by the prawn.

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Figures 27-34.—Right chelicerae of species of *A-us* from Timbuktu: 27, 29, 31, 33. Dorsal views; 28, 30, 32, 34. Prolateral views of moveable finger; 27, 28. *A-us x-us*, holotype male; 33, 34. *A-us y-us*, male. Scale = 1.0 mm.

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